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Larval Development of Shallow Water Barnacles of the Carolinas (Cirripedia: Thoracica) With Keys to Naupliar Stages

William H. Lang

February 1979

U.S. DEPARTMENT OF COMMERCE National Oceanic and Atmospheric Administration National Marine Fisheries Service

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U.S. DEPARTMENT OF COMMERCE

Juanita M. Kreps, Secretary

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National Marine Fisheries Service

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CONTENTS

Page

Introduction	1
Materials and methods	1
Larval development of barnacles	3
Definition and diagnostic characters	3
Larval descriptions	7
Balanus venustus Darwin	7
Balanus eburneus Gould	9
	13
	14
	17
Delener trian D	18
Conopea galeata (Linnaeus)	19
Chelonibia patula (Ranzani)	19
Chthamalus fragilis Darwin	22
	24
T	25
Nauplius SC	27
	29
Assigning stages	29
	31
	36
Discussion	36
	37
Literature cited	38

Figures

1.	Descriptive terminology of barnacle larvae							4
	Setation formulae for the mandible of stage IV Balanus eburneus nauplius							5
3.	Examples of barnacle larvae setal types							6
4.	Diagnostic morphological features of balanomorph nauplii at each stage							8
5.	Balanus venustus. Shield outlines							9
	Balanus venustus. Naupliar antennule and mandible							10
7.	Balanus venustus. Naupliar antenna							11
	Balanus venustus. Abdominal process and labrum							12
9.	Balanus eburneus. Shield outlines and abdominal process							13
	Balanus amphitrite amphitrite. Shield outlines, cyprid carapace profile, and							
	cess							14
11.	Balanus improvisus. Shield outlines							15
12.	Balanus improvisus Antenna, antennule, labrum, and abdominal process .							16
13.	Balanus subalbidus. Shield outlines, labrum, and abdominal process							17
14.	Balanus trigonus. Shield outlines							18
15.	Balanus trigonus. Antenna and mandible							19
16.	Balanus trigonus. Abdominal process and labrum							20
17.	Conopea galeata. Shield outlines, labrum, dorsal shield spines, and abdomin	na	1 1	oro	oce	ss		21
18.	Chelonibia patula. Egg, shield outlines, and carapace profile							21
19.	Chelonibia patula. Antennules							22
20.	Chelonibia patula. Antennae							23
21.	Chelonibia patula. Mandibles							24
22.	Chelonibia patula. Abdominal process and labrum							25
23.	Chthamalus fragilis. Shield outlines, lateral profile, and carapace outline .							26
24.	Chthamalus fragilis. Antennule, antenna, and mandible							26
25.	Chthamalus fragilis. Abdominal process and lateral profile							27
26.	Chthamalus fragilis. Labrum							27
27	Octolasmis muelleri Shield outlines							28

28.	Octolasmis forrestii. Shield outlines	28
29.	Octolasmis forrestii. Antennule, antenna, mandible, and labrum	29
30.	Lepas pectinata. Shield outlines and lateral profiles, abdominal spines, labrum, antennule, an-	
	tenna, and mandible	30
31.	"Nauplius SC." Shield outlines and lateral profiles	31
32.	"Nauplius SC." Antennule, antenna, and mandible	32
33.	Stage II nauplii of Balanus amphitrite-complex species common in Carolina waters	32
34.	Stage II nauplii of barnacle species found in Carolina waters	33
35.	Morphological features of Carolina barnacle nauplii	35
36.	Cyprids of South Carolina	36

Tables

1.	Thoracican Cirripedia of the South Carolina coast
2.	Studies on barnacle larval development
	Setal types of cirriped nauplii
4.	Typical setation counts for balanid nauplii
5.	Setation formulae for nauplii of Balanus venustus
6.	Setation formulae for nauplii of Balanus eburneus
7.	Size of Balanus eburneus and Balanus amphitrite larvae
8.	Setation formulae for nauplii of Balanus a. amphitrite
9.	Setation formulae for nauplii of Balanus trigonus
10.	Setation formulae for nauplii of Chelonibia patula
11.	Setation formulae for nauplii of Chthamalus fragilis
12.	Structure of the Octolasmis lowei-complex
13.	Setation formulae for nauplii of Octolasmis muelleri
14.	Setation formulae for nauplii Y
15.	Size ranges of barnacle nauplii obtained by laboratory rearing and plankton samples 34
16.	Size of barnacle cyprids reared in the laboratory
	Setal counts for the antennae of stage VI nauplii of some barnacle species

Larval Development of Shallow Water Barnacles of the Carolinas (Cirripedia: Thoracica) With Keys to Naupliar Stages¹

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ABSTRACT

The report includes an introduction to structure, descriptions, and illustrated keys to the barnacle larvae of Georgetown, S.C. Descriptions of 13 species are based on both laboratory reared and field specimens. The complete naupliar development of *Chelonibia patula*, *Chthamalus fragilis*, *Balanus* venustus, *Balanus subalbidus*, *Octolasmis forrestii*, and an unknown species, "nauplius SC," is described for the first time.

INTRODUCTION

The abundance and ability of barnacles to settle on virtually any solid substrate has made them a target of numerous detailed studies (see Newman and Ross 1976). Although the biology of many adult barnacles is relatively well studied, little information exists on the larval biology of cirripeds. This is particularly true of temperate and tropical species, as is evident by the limited information available for cirriped larvae along the southeastern coasts of the United States. Of over 25 species of thoracican cirripeds known to occur in South Carolina waters (Table 1), life histories are known for five species (Table 2) and the larvae of only two species, *Balanus amphitrite amphitrite* and *Balanus eburneus*, have been studied regionally (Costlow and Bookhout 1957, 1958).

This study was initiated to provide missing larval descriptions of common southeastern barnacle species and to construct a key for field identification of barnacle nauplii of coastal Carolina waters. In addition, some changes in descriptive terms and setation formulae are proposed.

MATERIALS AND METHODS

Adult barnacles were primarily collected in North Inlet and Winyah Bay near Georgetown, S.C. Of 11 species obtained in the Georgetown region (Table 1), larvae were reared for 10 species. Additional material for comparative purposes was collected at Pettaquamscutt Pond and Narragansett Bay, R.I., or obtained from Belize, Central America. Further details of collection sites and habitats are described in the introduction to the larval descriptions. Various methods and diets were used to rear barnacle larvae both to obtain material for descriptions and for diet-temperature studies (Lang³). In general, most descriptive material was obtained using rearing methods similar to those of Freiberger and Cologer (1966); however, antibiotics were not used and mixed algal diets were employed. Larvae were obtained from adult barnacles maintained in laboratory tanks and fed Artemia

³Lang, W. H. 1977. The barnacle larvae of North Inlet, South Carolina (Cirripedia: Thoracica). Unpubl. Ph.D. Thesis, Marine Science Program, Univ. South Carolina, Columbia, 179 p.

Table 1.—Thoracican Cirripedia of the South Carolina coast. (From Zullo and Lang 1978.)

Suborder Lepadomorpha	Suborder Balanomorpha
Lepadidae	Archeobalanidae
Lepas anatifera	A casta cyathus $(?)^1$
L. anserifera	Conopea galeata
L. hilli	C. merrilli
L. pectinata	
Conchoderma auritum	Glanaidae
C. virgatum	
	Balanus a. amphitrite
Scalpellidae	B. calidus
	B. eburneus
Scalpellum gibbum	B. improvisus
	B. reticulatus (?) ¹
Poecilasmatidae	B. subalbidus
	B. trigonus
Octolasmis hoeki	B. venustus
Octolasmis muelleri	
Trilasmis spp.	Chthamalidae
	Chthamalus fragilis
	Coronulidae
	Chelonibia patula
	C. testudinaria
	Platylepas hexastylos

Stomatolepas elegans

1(?) = probable occurrence.

⁴Contribution No. 188 of the Belle W. Baruch Library in Marine Science, University of South Carolina, Columbia, SC 29208.

²U.S. Environmental Protection Agency, Environmental Research Laboratory, Narragansett, RI 02882.

Species	Source	Stages	Locations and authors	Species	Source	Stages	Locations and author
Lepadomorpha							
Scalpellum scalpellum	г	all	Sweden (Kaufmann 1965)	Solidobalanus hesperius	p/r	I-VI	Washington (Barnes and
Pollicipes spinosus	r	all	New Zealand (Batham 1946a)				Barnes 1959b)
P. mitella	r	all	Japan (Yasugi 1937)	Boscia anglicum	r	all	United Kingdom (Moyse 196
P. polymerus	r	all	USA, west coast (Lewis 1975)	Balanus balanus	p/r	all	United Kingdom (Barnes an
Ibla idiotica	r	all	New Zealand (Batham 1946b)				Costlow 1961)
I. quadrivalvis	г	all	Australia (Anderson 1965)		р	all	North Atlantic (Crisp 1962a
I. cumingi	r	all	India (Karande 1974c)	Balanus crenatus	r	all	California (Herz 1933)
Lepas fascicularis	р	all	Pacific (Willemoes-Suhm 1876; Bainbridge and		p/r	all	United Kingdom (Pyefinch 1948)
			Roskell 1966)	B. nubilus	p/r	I-VI	Washington (Barnes and Barnes 1959a)
Verrucomorpha				B. amphitrite amphitrit	e r	all	Japan (Hudinaga and Kasaha
		7 3.77	United Kingdom (Dessindels				1942)
Verruca stroemia	p/r	I-VI	United Kingdom (Bassindale 1936)		р	I-II	South Africa (Sandison 1954
	p/r	I-VI	France (LeReste 1965)		r	all	Brazil (Lacombe and Mont 1972)
					р	all	India (Pillai 1958)
Balanomorpha (Chthamaloidea)					r	all	N. Carolina (Costlow and Bookhout 1958)
Chthamalus stellatus	p/r	I-VI	United Kingdom (Bassindale 1936)		r	alli	Florida (Freiberger and Cologer 1966)
	r	all	India (Daniel 1958)		r	all	India (Karande 1973)
	r	I-III	Brazil (Lacombe 1973)	B. a. abicostatus	r	I-VI	Japan (Ishida and Yasugi 1
C. dentatus	p	I-II	South Africa (Sandison 1954)	B. eburneus	r	all	N. Carolina (Costlow and
C. malayensis	r	all	India (Karande and Thomas 1976)		r	alli	Bookhout 1957) Florida (Freiberger and
Chamaesipho columna	r	all	New Zealand (Barker 1976)				Cologer 1966)
C. brunnea	r	all	New Zealand (Barker 1976)	B. improvisus	р	I-VI	United Kingdom (Jones and
Euraphia aestuarii	p	I-VI	West Africa (Sandison 1967)				Crisp 1954)
Euraphia depressa	r	I-VI	France (LeReste 1965)		r	all ¹	Florida (Freiberger and
Octomeris angulosa	p/r	I-VI	South Africa (Sandison 1954)				Cologer 1966)
(Coronulaidea)				B. variegatus	r	all	India (Daniel 1958)
Chelonibia patula	r	I-III	Brazil (Lacombe 1973)		r	all	India (Karande 1974a)
C. testudinaria	р	I-II	India (Pillai 1958)	B. pallidus stutsburi	р	I-VI	West Africa (Sandison 1954)
Tetraclita squamosa	r	all1	Japan (Hirano 1953)	B. trigonus	r	all	Japan (Hirano 1953)
T. serrata	р	I-II	South Africa (Sandison 1954)		p/r	I-VI	South Africa (Sandison 1954
Tetraclitella karandei (Balanoidea)	r	all	India (Karande 1974b)		r	all ¹	Florida (Freiberger and Cologer 1966)
Acasta spongites	r	all	United Kingdom (Moyse 1961)		r	all	New Zealand (Barker 1976)
Chirona hameri	p/r	all	United Kingdom (Crisp 1962b)	B. perforatus	р	all	United Kingdom (Groom
Conopea galeata	r	all	USA, west coast (Molenock and Gomez 1972)		р	all	1894-95) United Kingdom (Norris an
Eliminius modestus	р	all	United Kingdom (Knight-Jones and Waugh 1949)	Megabalanus algicola	p/r	all	Crisp 1953) South Africa (Sandison 1954
Epopella plicatus	r	all	New Zealand (Barker 1976)	M. t. tintinnabulum	r	I-III	Brazil (Lacombe 1973)
Semibalanus balanoides		I-VI	United Kingdom (Bassindale 1936)	m. r. ununnaoaiam	r	all	India (Daniel 1958)
	р	all	North Atlantic (Crisp 1962a)				
	r	all ¹	New York (Freiberger and Cologer 1966)				

¹Primarily methodology/rearing papers with limited descriptions.

(day old nauplii through adults), rotifers, and mixed algal cultures. Nauplii released from these populations were concentrated using a narrow light beam and removed with a pipette to 1 μ m filtered natural seawater between 25 and 32%. A double algal diet of *Tetraselmis* suecia (TET) in combination with *Monochrysis lutheri* (MON), *Isochrysis galbana* (ISO), *Thalassiosira pseudonana* (3H), or *Skeletonema costatum* (SKEL) was used as food. Further details of rearing techniques and diet results were described in Lang (1976, see footnote 3). Drawings of larvae were made with a camera lucid. When possible, freshly sacrificed larvae were used for in itial figures. The figures were verified using additionmaterial preserved in 70% ethanol or, more commonly Formalin and seawater. Measurements were made with an ocular micrometer on unflattened preserved larvae. Total length was measured from the anterior edge of the cephalic shield to the tip of the dorsal thoracic spins. Shield length was measured along the middorsal line from anterior to posterior shield borders, exclusive of lateral or posterior shield spines. Width was measured at the widest portion of the shield exclusive of frontolateral horns and shield spines. Cyprid length was measured from the anterior to posterior carapace margin. Cyprid "width" or depth was measured as the greatest distance from the dorsal to ventral carapace margins.

LARVAL DEVELOPMENT OF BARNACLES

The most common sequence of larval development for thoracican cirripeds consists of six naupliar and one cyprid stage. Using plankton reconstructions, Willemoes-Suhm (1876) and Groom (1894-95) reported six naupliar and one cyprid stage for both the lepadomorph Lepas fascicularius and the balanomorph Balanus perforatus. Herz (1933) reported eight naupliar stages from cultures of Balanus crenatus larvae however, Bassindale (1936), using both cultures and plankton material, found a consistent pattern of six naupliar stages and one cyprid stage for Verruca stroemia, Semibalanus balanoides, and Chthamalus stellatus. Most studies since then have confirmed this pattern of larval development (Table 2). A second study of B. crenatus yielded six naupliar stages (Pyefinch 1948). Conclusive proof of the number of larval stages was provided by the studies of Costlow and Bookhout (1957, 1958). Counts of molts of the larvae of Balanus eburneus and B. amphitrite amphitrite reared individually in small compartments consistently yielded the expected pattern of six naupliar and one cyprid stages.

A remarkably uniform pattern of cirriped larval development is evident. Adults release newly hatched nauplii which, within a short time span, molt to stage II nauplii. Further development (usually dependent on proper diet) produces four additional naupliar stages and the cyprid. The nonfeeding cyprid will select a substrate, settle, and undergo final metamorphosis to a juvenile.

Exceptions to this pattern of five planktotrophic naupliar stages are known. Nilsson-Cantell (1921) reviewed rather sparse observations on deepwater cirripeds in which the naupliar stage is passed through in the egg. Fully developed cyprid larvae or advanced metanauplii are released at hatching. Barnard (1924) found that over half (12 of 17) of South African Scalpellum species lack free-swimming naupliar stages; this characteristic appears to be independent of adult depth distributions. Complete naupliar development without feeding (lecithotrophic development) is also known, either with an irregular molt in nauplii and precocious cyprid development (Anderson 1965) or with six naupliar stages and cyprid (Kaufmann 1965).

DEFINITION AND DIAGNOSTIC CHARACTERS

As described by Groom (1894), the basic anatomy of the cirriped nauplius is well established (Kruger 1940; Walley 1969). Walley (1969) extended Groom's observations on the internal anatomy of the nauplius (Semibalanus balanoides), but notable additions to the external morphology of larvae will probably rest on scanning electron microscopy (EM) studies, such as those recently reported by Walker (1973, 1974a) and Rainbow and Walker (1976).

As a guideline to descriptions presented in this study, a summary of external morphology and taxonomic characters of cirriped larvae follows. Although in most cases this represents a simple review of past literature, some basic changes in terminology of larval structures and setal types are proposed.

The dorsal surface of the nauplius (Fig. 1A, B) is composed almost entirely of a unitary carapace shield (Anderson 1973) or correctly, the cephalic shield (cs), with a pair of prominent frontolateral horns (fh) anteriorly and a dorsal thoracic spine (DTS) posteriorly. Ventrally, there are three pairs of jointed appendages: the antennules (An1), the antennae (An2), and the mandibles (Mn). A pair of unjointed filiform appendages-the frontal filaments-extend anteriorly between the antennules. A prominent labrum (lb) lies between the antennae and overhangs the mouth. The posteroventral "postnaupliar region" (Anderson 1973) consists of the abdominal process (AP) which terminates with the furcal spines. The ventral surface between the mouth and postnaupliar region has a complex array of small processes referred to as the setose region. It includes the maxillary portion of the cephalon and the incipient thorax.

Cephalic shield. Despite the virtually universal reference to the naupliar carapace in the literature, the nauplius, by definition, lacks a true carapace (Anderson 1973; Moore and McCormick 1969; Newman pers. commun.). In naupliar stages I-III the shield tapers directly into the DTS. At stage IV, a distinct posterior shield (ps) border is formed (see Fig. 5); this border usually has two ps spines (see Fig. 4 IV-VI). The shield may also have dorsal and/or lateral spines or lack spines entirely.

Frontolateral horns. These distinctive structures are unique to cirriped nauplii, although their function remains unknown (see Walker 1973). Their relative size or orientation is often characteristic of the species or family. Stage I nauplii have fh folded back along the carapace, but beginning with stage II, the horns are extended in an anterolateral direction. Willemoes-Suhm (1876) noted fine setae extending from between the spined tips of fh in *Lepas* larvae, however, using scanning EM, Walker (1973) described shredded cuticle at the same location for several balanomorph species.

Dorsal thoracic spine. Commonly called the "caudal spine" this process originates dorsal to the thoracic anlage of the nauplius. Since the caudal furca of cirriped nauplii, and of the cyprids, is homologous to the "caudal spines" of copepod and other crustacean nauplii (Anderson 1973), the classical term is misleading. As suggested by W. A. Newman, DTS has been adopted. Nearly always present and often barbed or serrate, the DTS is greatly elongated in lepad species and least developed in

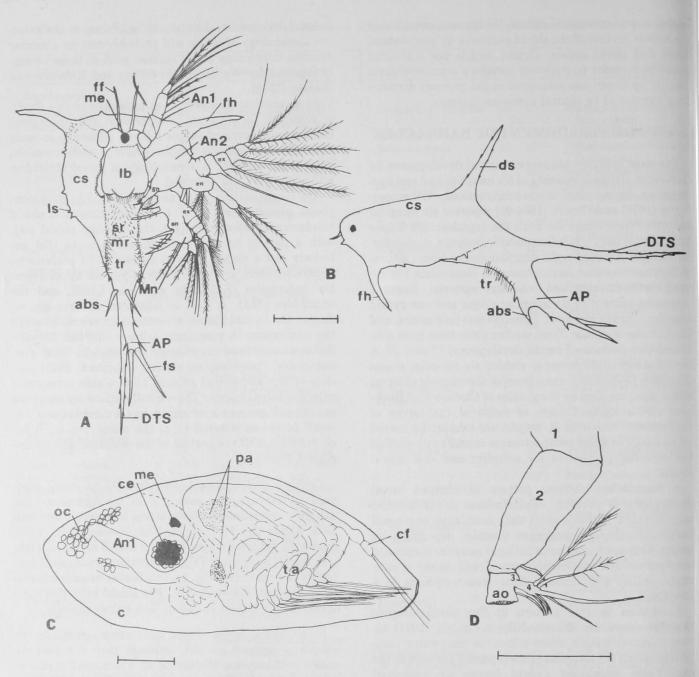


Figure 1.—Descriptive terminology of barnacle larvae: ventral view (A) and lateral view (B) of *Conopea galeata* stage II nauplius; *Chelonibia patula* cyprid (C) and detail of the antennule (D). abs, abdominalspines; An1, antennule; An2, antenna; AP, abdominal process; ao, adhesive organ (on the third segment of An1); ce, compound eye; cf, caudal furca; cs, cephalic shield; ds, dorsal shield spine; DTS, dorsal thoracic spine; en, endopodite; ex, exopodite, ff, frontal filament; fh, frontolateral horn; fs, furcal spines; gn, gnathobase; lb, labrum; ls, lateral shield spines; me, median or naupliar eye; Mn, mandible; mr, maxillary region; oc, oil cells; pa, pigmented area; sr, setose region; ta, thoracic appendage; tr, thoracic region. All scales = 0.1 mm.

chthamalid larvae. Its relative length compared with shield and AP may provide diagnostic characteristics.

Frontal filaments. Recently studied by Kauri (1962, 1966), and Walker (1974a), their function remains debated. Often closely folded to the body wall in stage I nauplii, with the exception of some chthamalid species, the filaments are evident in all subsequent naupliar stages.

Jointed appendages. The An1 is uniramous and consists of four segments in late naupliar stages. The An2 is biramous, the endopod and exopod arising from a twosegmented base. By stage VI the exopod (= exopodite) consists of nine segments and the endopod (= endopodite) is three-segmented. Similar to the antenna, the Mn is biramous with a two-segmented base, two-segmented endopod, and five-segmented exopod.

Labrum. The lb is relatively large and rigidly fixed to the body above the mouth. The shape of the free end appears to be a useful family characteristic.

Maxillary and thoracic regions. The setose region, posterior to the true mouth and extending to the abdominal spines, is divided in two: the anterior maxillary and posterior thoracic regions. Rudimentary maxillae and anlage of the thoracic appendages will be evident in later naupliar stages. Functional appendages first appear in the cyprid.

Abdominal process. The AP arises from the ventroposterior body region and terminates in a stem bearing spines of the caudal furca. Pairs of lateral abdominal spines appear at stage II and increase in number with subsequent molts. Norris and Crisp (1953) defined three sets of serially homologous spines which develop in a highly predictable order in balanid larvae (Fig. 4).

Setation. Setae are well developed on the limbs and ventral body regions, serving both a natatory and feeding function (Gauld 1959). The number and types of setae are fundamental morphological characters which are, in part, used for determining the naupliar stage (Fig. 4, Table 4) and, to a lesser extent, the species.

Bassindale (1936) initiated use of a setation formula similar to that used for copepod appendages. The formula specifies only setal numbers and location. Jones and Crisp (1954) devised a graphical method to show setal numbers, types, and relative lengths. Newman (1965) combined the simplicity of Bassindale's formula with the informational content of the Jones and Crisp graphics to create an alphabetical notation. Sandison (1967) further modified Newman's system, adding additional setal types and using numerical groupings of similar setae. For a comparison of these setation formulae, see Figure 2.

The basic setation formula of Newman (1965) is used in this study with some modifications. The initial four setal types of cirriped larvae defined by Jones and Crisp (1954) and Newman (1965) were expanded to seven types by Sandison (1967) (Table 3). A similar but independent trend to define specific setal types in decapod larvae was initiated by Bookhout and Costlow (1974), their setal types based on the definitions of crayfish setae by Thomas (1970). Essentially two problems now exist: 1) additional setal types undefined by Sandison (1967) have been observed in the present study, and 2) there are two sets of terms used for respective cirriped and decapod setal types. This latter situation does not seem warranted based on comparative observations on decapod larvae (Lang and Young 1977; Johns and Lang 1977).

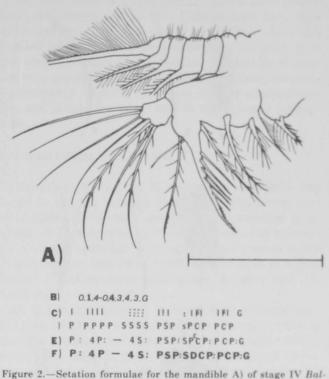


Figure 2.—Setation formulae for the mandible A) of stage IV Balanus eburneus nauplius; B) formula of Bassindale (1936); C) formula of Jones and Crisp (1954); D) formula of Newman (1965); E) formula of Sandison (1967); F) formula used here (see also Table 3). Scale = 0.1 mm.

Bookhout and Costlow (1974) organized the setal terminology and descriptions of Thomas (1970) into seven basic groups for describing the larvae of *Portunus spinicarpus*. Four of these groups appear to apply equally to cirriped larvae:

- Simple setae are acuminate with no setules or projections.
- Plumose setae possess fine hairlike setules coming off opposite sides of the shaft.
- Plumodenticulate setae bear hairlike setules on the basal part of the shaft and fine or stout denticules on the distal portion.
- Cuspidate setae have enlarged bases and stout shafts tapering to a point. These may be further

Jones and Crisp (1954) Symbol-Type	Newman (1965) Symbol-Type	Sandison (1967) Symbol-Type	Present Symbol-Type
: without setules	S - simple	S - simple	S - simple
with setules	P - plumose	P - plumose F - feathered	P - plumose F - feathered
		P ^c - setose, serrate tip	D - plumodenticulate B - bristled
F comb-like	C - combed	C - combed H - hispid	C - cuspidate H - hispid
G - gnathobase	G - gnathobase	G - gnathobase	G - gnathobase
simple or plumose	S' - S, sometimes P	S' - S, sometimes P	S ^P - S, sometimes P
	P' - P, sometimes S	P' - P, sometimes S	P ⁸ - P, sometimes S

Table 3.-Setal types of cirriped nauplii.

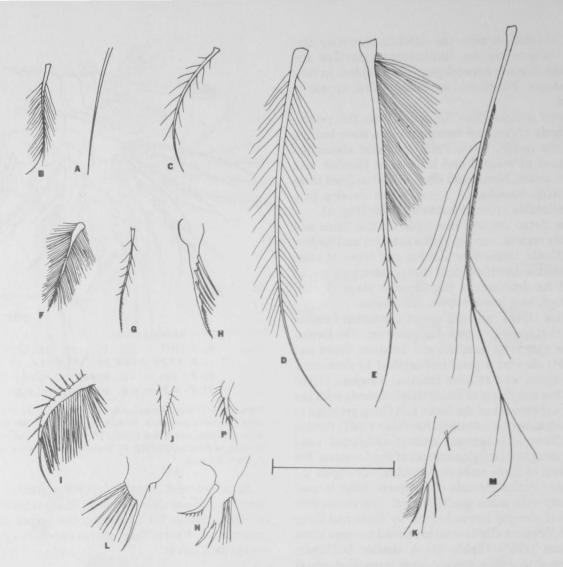


Figure 3.—Examples of barnacle larvae setal types: A) simple; B-E) plumose; F) feathered; G) plumodenticulate; H-K) cuspidate; L) hispid; M) bristled; N, P) gnathobases. Scale = 0.1 mm.

specified as denticulate, cuspidate, or plumodenticulate cuspidate types.

Incorporation of these groups, setal types described by Sandison (1967), and present observations, result in the following setal types used in this paper:

- Simple (S): setae with no setules or projections (Fig. 3A).
- Plumose (P): setae with fine hairlike setules, short or long, usually but not always coming off opposite sides of the shaft (Fig. 3B, C, D, E).
- Feathered (F): plumose setae with dense "downy" setules and flattened spatulate shaft (Fig. 3F).
- Plumodenticulate (D): plumose setae with denticulate or serrate tip (Fig. 3G).
- Cuspidate (C): setae with enlarged base and stout shaft tapering to a point. The presence of stout to fine denticules, often comblike in orientation, is typical (Fig. 3H, I, J, K).

Hispid (H): cuspidate setae with flattened modified shaft (Fig. 3L).

Bristled (B): plumose setae with basal portions of shaft serrate or "bristled" (Fig. 3M).

The gnathobase (G) is classically defined as a rigid toothed or "biting" process and is located on the basal segment of both An2 and Mn in cirriped larvae. Rainbow and Walker (1976) also refer to the An2 endopod cuspidate seta (Fig. 3K) as a G. It should be noted that the An2 G is a unique structure (Fig. 3N) while the Mn G (Fig. 3P) differs little from other cuspidate setae. By convention, any rigid process on the basal segment of the appendages will be considered a G; setae at other locations will be classified as one of the above listed types.

Semantics and definitions of setal types have been somewhat altered from those listed by Sandison, but only one symbol has been changed ($P^c=D$), thus eliminating the superscript and repeated use of P. Feathered setae described by Sandison (Fig. 3E) for chthamalid larvae, often closely resemble postaxial plumose setae (An2, endopod) of some balanid larvae, but feathered setae have a distinct "spatulate shaft"; and enlarged flattened basal region is obvious. Similarly, the 'bristled'' proximal shafts of some An1 setae of Octoasmis and Lepas larvae are quite distinctive; a new setal type (bristled) has been introduced.

Superscripts will be used to designate setal type variapility. Thus, P^s infers plumose seta, sometimes simple; S^p, simple seta, sometimes plumose; P^D, plumose seta, sometimes plumodenticulate; etc.

The cyprid larva (Fig. 1C) is enclosed by a bivalved carapace. The carapace may appear textured or sculpcured in some species, but is relatively smooth in all Carolina species examined. Using scanning EM, numerous small sensory setae and the fh pores are evident on the carapace surface (Walker and Lee 1976).

The naupliar An2 and Mn are transient structures in the cyprid and are reduced to rudimentary groups of cells during the metamorphosis from nauplius to cyprid (Waley 1969). The An1, however, is retained as the primary sensory and attachment structure. Antennule setation is greatly reduced and a prominent attachment organ is present (Fig. 1D). Nott and Foster (1969) studied the An1 of *Semibalanus balanoides* cyprids in detail and concluded that attachment probably occurs by an adhesive disc. At the level of light microscopy, the An1 shows little variation between different species.

Propulsion is provided by six pairs of biramous thoracic swimming appendages. Their embryonic development is clearly evident in the basal region of the AP in stage VI nauplii. The articulate rami of the furca has complex sensory processes and perhaps aids in contour assessment (Walker and Lee 1976).

The internal anatomy of the cyprid has been reviewed and studied by Walley (1969). Structures readily evident in examination of whole specimens include: the naupliar eyespot, paired compound eyes, various pigmented areas, and oil cells.

LARVAL DESCRIPTIONS

All cirriped species studied at North Inlet exhibit the typical larval development of six planktotrophic naupliar and cyprid stages. The newly hatched stage I nauplius is nonfeeding and capable of only weak swimming activity. This stage rapidly molts to planktotrophic stage II; it is rarely encountered in plankton tows. The remaining five naupliar stages and cypris comprise the normal planktonic component of the cirriped life cycle and will be the main concern of the following descriptions and key.

With each molt the nauplius increases in size and complexity. All known planktotrophic balanomorph nauplii exhibit basic morphological changes at each molt which allows the accurate staging of any species. A diagrammatic outline of key morphological features is presented in Figure 4; these features will be considered the "normal" developmental sequence. Of North Inlet species, only Octolasmis larvae differs significantly from this pattern (Lang 1976).

Setation of the naupliar appendages is also quite uniform among most balanid species. Based on a review of existing descriptions (Table 2), the "normal" or expected setal counts are indicated in Table 4. Setal counts between different species vary little in most instances; variations in setal types occur more often. Although detailed studies of setae serve little practical use in routine staging or identification of larvae, details of setation may provide useful information for studies concerning taxonomy, regional variations, feeding mechanisms, etc., and should not be ignored in initial larval descriptions.

Balanus venustus Darwin

Darwin's (1854) variety *B. amphitrite amphitrite* was raised to specific rank by Harding (1962). Henry and McLaughlin (1975) considered Darwin's varieties *B. a. niveus*, *B. a. modestus*, and *B. a. obscurus* as synonymous with *B. venustus*. Although confusion exists in the early literature (see Zullo 1966), *B. venustus* is a predominant shallow-water subtidal species from New England to Florida.

All specimens collected in North Inlet (Georgetown, S.C.) were found in subtidal habitats. *Balanus venustus* was the predominant species on all subtidal debris: wood, metal, plastic, glass, shells (but not oyster beds). It was abundant on hermit crab shells and occasionally on the carapace of horseshoe crabs; spider crabs, *Libinia emarginata*; and blue crabs.

Although *B. venustus* is a common species, no descriptions of its larvae seem to exist. Numerous hatches of larvae were successfully reared; adults used to obtain larvae for the following descriptions were positively identified by Dora Henry.

Stage I. (Fig. 5A). Typical stage I nauplius with rudimentary AP and DTS; fh folded rearward, but rarely collapsed completely against body.

Stage II. (Fig. 5B). Frontolateral horns extended nearly perpendicular to median body axis; anterior shield (as) margin slightly convex to flat; DTS and AP well developed, distinctly barbed. Spination quite distinct; anterior margin of shield with four small lateral spines, side margins with four pairs of similar spines, and one larger spine pair at future location of ps margin; one short median dorsal spine also present. Entire shield margin spinulose (numerous minute spines present).

Stage III. (Fig. 5C). Frontolateral horns directed slightly forward; as margin slightly arched with two small lateral spines, spinulose margins, and closely spaced pair of median dorsal spines. Maxillules represented by one stout simple seta (see Fig. 8B).

Stage IV. (Fig. 5D). Shield marginal spination further reduced to a variable number of small lateral spines and spinulation; paired dorsal spines similar to stage III. Posterior shield margin present; ps spines straight, relatively stout. The DTS is long, generously barbed; AP with series two spine pair and single well-developed median spine (see Fig. 8C).

Stage V. (Fig. 5E). Very similar to stage IV. Shield margin spinulose, no larger lateral spines present; paired dorsal spines widely spaced and minute. Series three

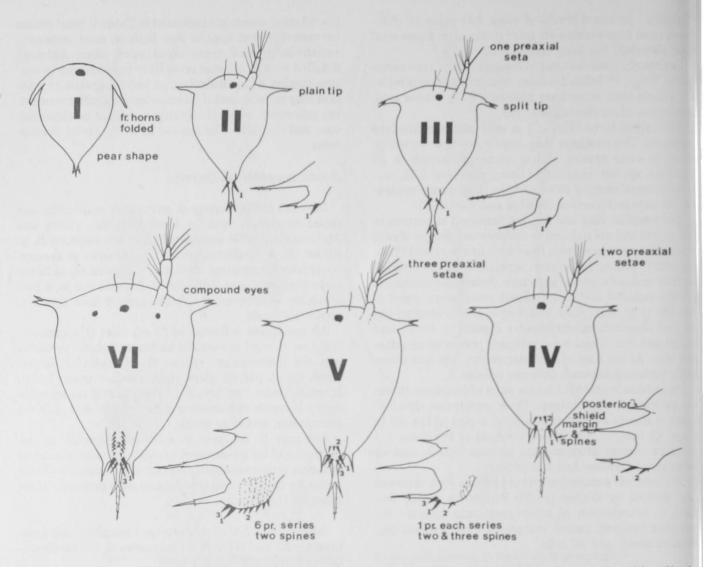


Figure 4.—Diagnostic morphological features of balanomorph nauplii at each stage. Abdominal spine designations are adapted from Norris and Crisp (1953) and Moyse (1961).

Table	41	ypical	setation	counts	IOL	balanid	naupilli.	

Stage	Antennule	Antenna	Mandible
Ι	0.4.2.1.1	0.1.4-0.3.2.2.2.G	0.1.3-0.3.2.2.2.G
II	0.4.2.1.1	0.2.5-0.3.2.2.3.G	0.1.4-0.3.2.3.2.G
Ш	1.4.2.1.1	0.2.5-0.3.2.2.4.G	0.1.4-0.3.3.3.3.G
IV	1.1.4.2.1.1	0.3.6-0.5.3.2.4.G	0.1.4-0.4.3.4.3.G
V	1.1.1.4.2.1.1.1	() ¹ 0.5.3.2.4.G	0.1.5-0.4.4.4.3.G
VI	1.1.1.4.2.1.2.1	() ² 0.5.3.2.4.G	0.1.5-0.4.4.4.3.G

Variable configuration with a total of 10 or 11 setae.

²Variable configuration with a total of 11 or 12 setae.

spine pair present on AP; series two pair and median spine as in stage IV (see Fig. 8E, F).

Stage VI. (Fig. 5F). Spinulation of shield margin often indistinct; most evident on anterior and posterior margins. The ps spines reduced in length but stout; DTS long and well armed.

Cyprid. Virtually identical to *B. improvisus* (Jones and Crisp 1954). No apparent distinctive characteristics.

Characteristic morphological features associated with each balanid naupliar stage (Fig. 4) are closely followed in the larval development of *B. venustus*. Lateral shield spination is somewhat variable; in some hatches the lateral shield spines are less distinct and generally smaller.

Setation of the naupliar stages (Table 5) closely follows the normal balanid pattern (Table 4). The first preaxial seta of An1 is plumose at stage III (Fig. 6C), as

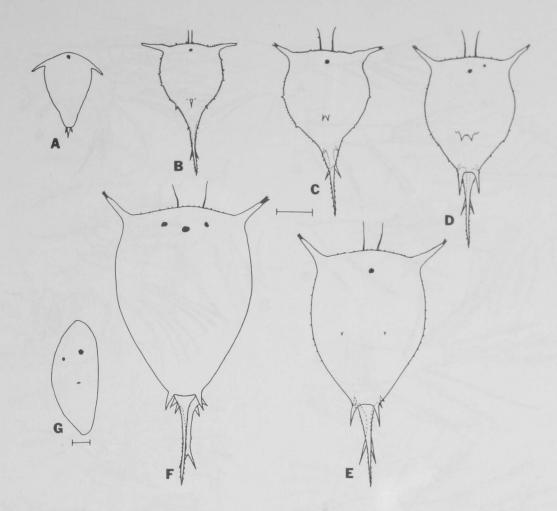


Figure 5.—Balanus venustus. Shield outlines of stages I-VI (A-F) and cyprid carapace profile (G). Scales = 0.1 mm.

Table 5Setation formula	for nauplii	of Balanus	venustus.
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Stage	A	nl					_		Ar	12						Μ	In		
VI	SPPPSPF	SPI	PPS	s	3P 8P	PP	SPF	PS	SP	PD	PCP	G	P 5P	4S D	SPS	D	SCP	PCP	G
V	SPPPSPF	SP	SP	S	3P 6PS	PP	SPF	PS	SP	PD	PCP	G	P4PS	4S D	SPS	D	SCP	PCP	G
IV	SPPSPF	SP	Р	S	2P 6PS	PP	SPS	PS	SP	PD	PCP	G	P4P	4S D	SS	Po	SCP	PCP	G
III	P PSPF	SP	Р	S	2P 5P	PP	Ρ	Р	s	PD	PCS	G	P 3PS	3SP	SS	Po	CP	PCP	G
П	SSPS	SP	Р	S	SP 4PS	PP	S	Ρ	S	PD	PC	G	P 3PS	3SP	S	P	CS	PC	G
I	SSSS	SS	S	s	S 4S	SS	S	s	S	SS	SS	G	S3S	3S S	S	S	S	SS	G

opposed to a simple seta in many species. The first postaxial setal group of the Mn endopod has one to two plumodenticulate setae beginning with stage III (Fig. 6I, J). The An2 exopodal setae are relatively stout; the endopod is well developed, with one less seta than expected (stages III-VI) in the last postaxial setal group adjacent to the G (Fig. 7).

The DTS remains notably long in late stage nauplii and is distinctly barbed in all stages (II-VI). The AP is also well developed but remains shorter than the DTS; abdominal spines are stout and easily observed (Fig. 8A-G). Maxillule setation first appears at stage III and increases to six (5 long, 1 short) stout simple setae by stage VI.

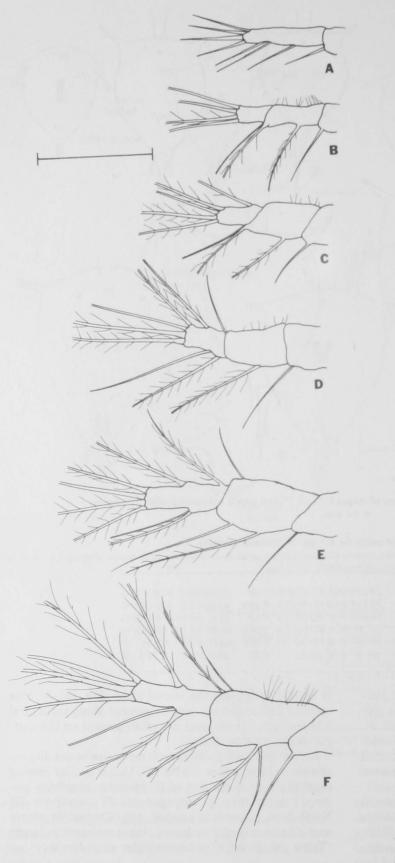
The lb is trilobed, the median lobe even with or slight-

ly extending beyond the lateral lobes (Fig. 8H-J). Fine teeth or denticulations may be present along the lateral lobe margins. Three teeth are often present on the margin of the median lobe.

Larvae increase in size at each molt; size variability increases in later stages (Table 15). Under similar rearing conditions the mean size of *B. venustus* nauplii is distinctly larger than *B. eburneus* and *B. amphitrite*. Of North Inlet balanids examined, only *Chelonibia patula* and *Conopea galeata* larvae are consistently larger (Table 15); *B. trigonus* have similar sized larvae.

Balanus eburneus Gould

Balanus eburneus ranges from New England to Brazil in the western Atlantic and occurs from low water to 37



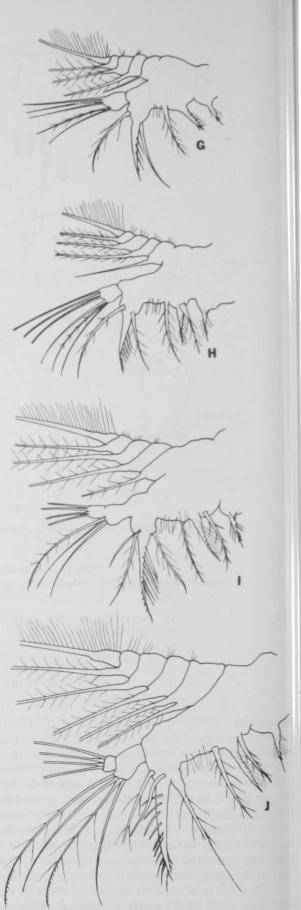


Figure 6.—Balanus venustus. Naupliar antennule of stage I (A), II (B), III (C), IV (D), V (E), VI (F); naupliar mandible of stage II (G), III (H), IV (I), VI (J). Scale = 0.1 mm.

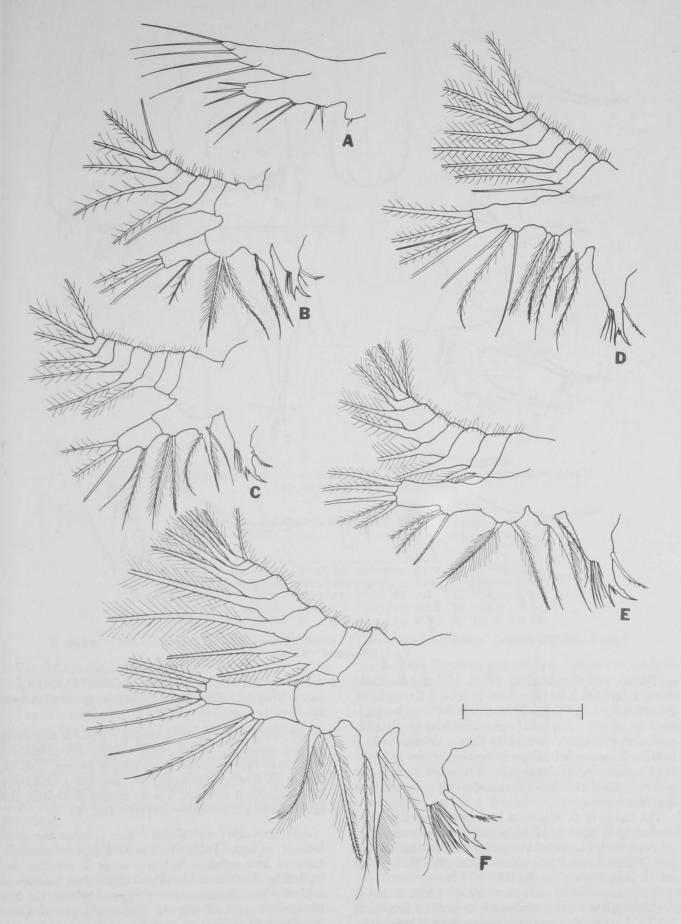


Figure 7.—Balanus venustus. Naupliar antenna of stage I (A), II (B), III (C), IV (D), V (E), VI (F). Scale = 0.1 mm.

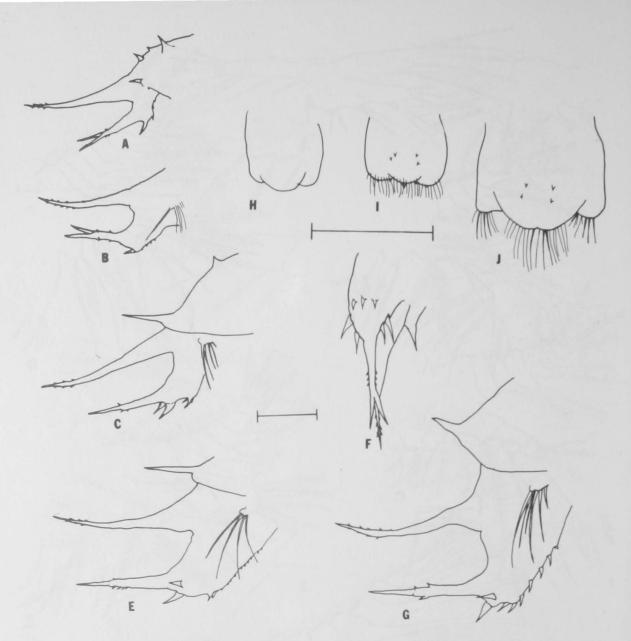


Figure 8.—Balanus venustus. Abdominal process of stage II (A), III (B), IV (C), V (E, F), VI (G); labrum of stage I (H), II (I), IV (J). Scales = 0.1 mm.

m (Henry and McLaughlin 1975). McDougall (1943) noted it is the most abundant intertidal barnacle at Beaufort, N.C. At North Inlet, *B. eburneus* is predominant on all intertidal wood structures from about midtide level and below. It rapidly fouls wood and plastic boat surfaces and is common on both intertidal and subtidal oysters. Intertidal specimens tend to be crowded and cylindrical in form while subtidal specimens, far less abundant, are conical.

The larvae of *B. eburneus* have been reared and described by Costlow and Bookhout (1957) using eggs from adults collected at Beaufort. Larvae were also reared, but not described, by Freiberger and Cologer (1966) using adults collected at Miami, Fla.

Numerous cultures of *B. eburneus* have been reared at South Carolina for this study and for work by Jorgensen (1976). Larval morphology closely matches results re-

ported by Costlow and Bookhout (1957) in major features; however, numerous discrepancies in setation were noted.

The shield of *B. eburneus* nauplii is plain in all stages, lacking dorsal or lateral shield spines. Morphological changes at each molt follow the normal pattern (Fig. 4). The fh are moderate in length and, beginning with stage II, are directed forward. The as margin is arched; the shield outline is smoothly elliptical (Fig. 9).

Setal formulae for all stages (Table 6) follow the usual balanid pattern (Table 4). Based on present observations of four separate hatches, stage II setation described by Costlow and Bookhout (1957) does not appear typical. Plumodenticulate setae are present on the Mn endopods (stages IV-VI); up to four plumodenticulate setae may be present at stage VI.

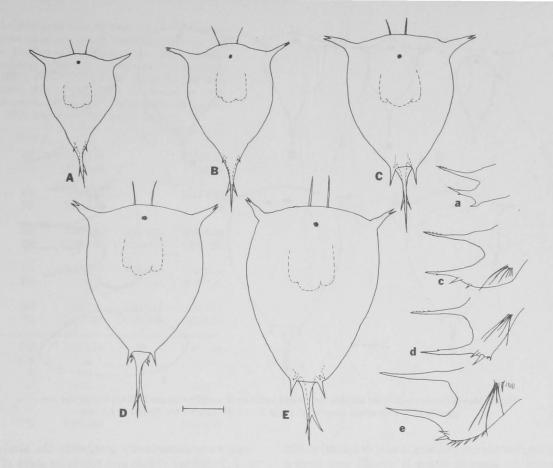


Figure 9.—Balanus eburneus. Shield outlines of stages II-VI (A-E); abdominal process of stage II (a), IV (c), V (d), VI (e). Scale = 0.1 mm.

Table 6.-Setation formulae for nauplii of Balanus eburneus.

Stage	An1				An2 Mn	
VI	S P P PSPP SF	PPS	SS	4P 8P	PPSPP PSP PD PSCP G P4PP 4S SDSD DSCD	P PCP G
V	S P P PSPP SF	SP	S	3P7PS	PPSPP PSP PD PSCP G P4PS 4S SDSD DSCD	PPCPG
IV	S P PSPP SF	P P	S	$2P 6PP^{s}$	PPSP* PSP PD PSCP G P4P 4S DSP DSCD	P PCP G
III	S PSPP SH	P	S	2P 5P	PP P PS PDPSCSG P3PS 3S PSS D CP	PCP G
П	SSPS SF	P	S	SP 4PS	PP S PS PDP CSG P3PS 3S PS P CS	PC G

The DTS is distinctly longer than the AP in all stages (Fig. 9a-e). Abdominal spination is typical (Fig. 4); one median spine is present in stages IV and V.

The lb is trilobed with a distinctly longer median lobe. Although the median lobe margin may have minor denticulation, no distinct teeth are present.

Balanus eburneus nauplii are generally small, averaging slightly larger than B. a. amphitrite larvae (Table 15). Size ranges of larvae reared at 25°C are similar to those reported by Costlow and Bookhout (1957) except for width.

Balanus amphitrite amphitrite Darwin

Balanus amphitrite amphitrite is a cosmopolitan species of warm and temperate seas. It is usually intertidal, often in brackish water. On the eastern coast of the United States, *B. amphitrite* is common from Florida north to the Carolinas and has been reported as far north as Massachusetts (Zullo 1963). At North Inlet, it is a common intertidal species, generally situated between upper intertidal *Chthyamalus fragilis* and lower intertidal *B. eburneus* on wood pilings.

The complex and often confused status of B. a. amphitrite has been reviewed by Henry and McLaughlin (1975). Of particular significance for a review of existing literature is the placement of B. a. communis, B. a. denticulata, and B. a. hawaiiensis in synonymy with B. a. amphitrite.

Costlow and Bookhout (1958) described larvae reared from North Carolina adults. Larvae have also been described from Japan (Hudinaga and Kasahara 1942), Brazil (Lacombe and Monteiro 1972), and India (Pillai 1958; Karande 1973). *Balanus a. amphitrite* larvae obtained from numerous diet and temperature studies have been compared with these existing descriptions.

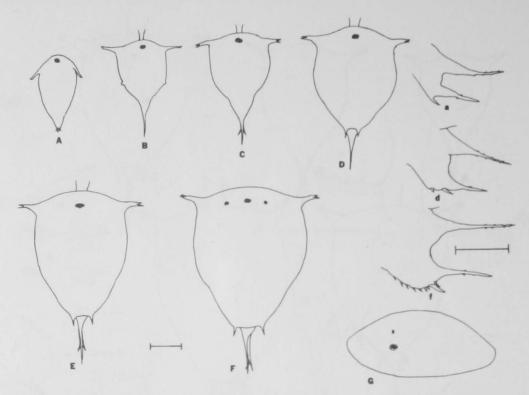


Figure 10.—Balanus amphitrite amphitrite. Shield outlines of naupliar stages I-VI (A-F); cyprid carapace profile (G); abdominal process of stage II (a), IV (d), VI (f). Scales = 0.1 mm.

Balanus amphitrite nauplii lack dorsal or lateral shield spines, except for stage II. Stage II nauplii may have a pair of small blunt spines on the lateral shield margin (Fig. 10B). Morphological changes at each molt are typical (Fig. 4). At stage II, the fh extend nearly perpendicular to the shield midline; the fh tips often bend slightly rearward. This configuration remains consistent in later stages (Fig. 10).

Setation is typical (see Table 8). The An2 exopod setae of stage VI nauplii are variable (11P, 11PS, 12P). Mandibular plumodenticulate setae are not well developed and only one such seta occurs consistently.

The DTS is longer than the AP in all stages (Fig. 10a, d, f). Abdominal spination is typical; one median spine is present in stages IV and V.

The lb is trilobed; the median lobe normally extends slightly beyond the lateral lobes. All lobes have numerous simple setae, but no teeth are present.

Balanus amphitrite larvae are small (Table 7), generally intermediate in size between *Chthamalus fragilis* and *B. eburneus* (Table 15). The rearward orientation of the fh is the most useful character for recognition of later stage nauplii. Stage II nauplii are readily confused with those of *B. improvisus;* care must be taken to note the small lateral spines and lack of distinct labral teeth for *B. amphitrite* larvae. Cyprids are very similar to those of other *amphitrite*-complex species; no means to identify this stage to species has been devised.

Present observations vary in numerous aspects from existing descriptions of B. *amphitrite* larvae. The size of larvae reported by all investigators (Table 7) is in general agreement, with two exceptions: the widths of all stages are consistently greater in the study of Costlow and Bookhout (1958) and the later stage (IV-VI) larvae reported by Pillai (1958) are relatively small and show little increase per molt. Interestingly, Pillai's work represents the only study using planktonic material; the smaller sizes could represent a real phenomenon, but observational error is more likely using planktonic material.

Setation of larvae does not completely agree in any study. It unfortunately is conjecture as to what degree this represents observational error in descriptions or real variation in the larvae. With the exception of the stage III Mn exopod, present setal counts agree with those of Costlow and Bookhout (1958). The descriptions of Hudinaga and Kasahara (1942) and Pillai (1958) are sufficient to allow generation of comparative setal formulae (Table 8). As indicated in the table, only three minor points of difference exist between the Japanese description and the present study. However, in the study by Pillai, stages V and VI setation shows significant variation. This sheds further doubt on the accuracy of his plankton identification.

Karande (1973) reports no median spine on the AP of stages IV and V. Hudinaga and Kasahara (1942) and Costlow and Bookhout (1958) make no mention of one, however, in agreement with present observations; Pillai (1958) reports a single median spine for both stages.

Balanus improvisus Darwin

Balanus improvisus occurs along the entire Atlantic coast of the United States and is found from the intertidal zone to 46 m (Henry and McLaughlin 1975). The Table 7.—Size of Balanus eburneus (top) and Balanus amphitrite (bottom) larvae reported from various sources: Costlow and Bookhout (1957) (BB); Costlow and Bookhout (1958) (CC); Hudinaga and Kasahara (1942) (HK); Karande (1973) (K); Lacombe and Monteiro (1972) (LM); Pillai (1958) (P); Sandison (1954) (S); and present results (PR). Total length (TL), shield length (SL), and width (W) in millimeters.

Stage	Source	TL	SL	W
П	BB	0.32-0.34		0.21-0.23
	PR	0.32-0.36		0.16-0.18
				0.10 0.10
III	BB	0.35-0.38		0.23-0.27
	PR	0.36-0.41		0.18-0.23
IV	BB	0.40-0.42	0.30-0.33	0.27-0.32
	PR	0.42-0.45	0.30-0.33	0.23-0.25
v	BB	0.44-0.48	0.35-0.38	0.29-0.34
	PR	0.46-0.57	0.33-0.44	0.26-0.32
	In	0.40-0.07	0.55-0.44	0.20-0.32
VI	BB	0.54-0.60	0.42-0.50	0.36-0.39
	PR	0.57-0.62	0.39-0.46	0.32-0.37
П	CC	0.25-0.30		0.19-0.24
	HK	0.26		0.16
	K	0.30		
	LM	0.31		0.15
	Р	0.29		0.16
	S	0.32		0.16
	PR	0.28-0.34		0.12-0.16
Ш	CC	0.30-0.34		0.22-0.27
	HK	0.30		0.22-0.27
	LM	0.38		0.19
	P	0.36		0.17
	PR	0.31-0.36		0.19
	rn	0.31-0.30		0.16-0.20
IV	CC	0.35-0.39	0.25-0.32	0.25-0.32
	PR	0.33-0.40	0.24-0.30	0.17-0.23
v	00	0 11 0 15	0.00.0.05	0.05.0.00
V	CC	0.41-0.47	0.30-0.35	0.25-0.32
	PR	0.40-0.47	0.28-0.35	0.24-0.28
	Р		0.27	0.27
VI	CC	0.47-0.53	0.35-0.40	0.35-0.43
	PR	0.47-0.57	0.34-0.39	0.27-0.32
		0111 0101		
	Р		0.29	0.27

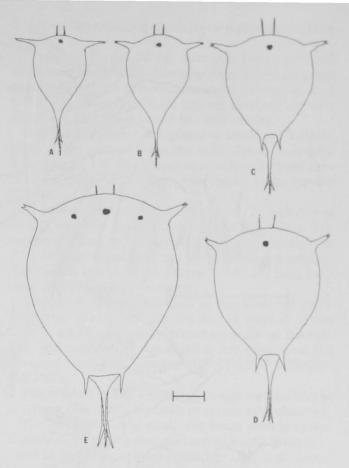


Figure 11.—Balanus improvisus. Shield outlines of naupliar stages II-VI (A-E). Scale = 0.1 mm.

species can withstand low salinities, is predominant in brackish water, and is often associated with *B. subalbidus* or, in Europe *Eliminius modestus* (Jones and Crisp 1954). In North Inlet, *B. improvisus* was conspicuously absent in the major tidal creeks with salinities generally above 20% but was common in waterways draining abandoned ricefields and also upper Winyah Bay, usually attached to concrete, bricks, or debris.

Table 8.—Setation formulae for nauplii of *Balanus a. amphitrite* as reported in different studies. Complete formulae for the present study (Pr) are given; differences from these formulae as derived from descriptions by Hudinaga and Kasahara (1942) (HK) and Pillai (1958) (PL) are noted.

Stage	Study	Anl		An2	Mn						
	Pr	S S P PSPP SP PPS	s	3P 9P PPSPP PSS PD PSCP G	P4PS ^p 4S PSPS DSCP PCP G						
VI	HK										
	PL			3P 7PS PP PP	P4PS						
	Pr	S S P PSPP SP S P	s	3P 7PS PPSP ^P PSS PD PSCP G	P4PS 4S PSPS DSCP PCP G						
V	HK			PPSPP PPS							
	PL	S P PSPP SP P	S	2P 6PS PP PP PPS PD PPCP G	P5P						
	Pr	S P PSPP SP P	s	3P 5PS PPSPS PSS PD PSCP G	P3PS ^p 4S PSP DSCP PCP G						
IV	HK	SSPSPPSP P	S	PPSPP	PPS						
	PL			2P 6PS PP PS PPCP	P4P						
	Pr	S PSPP SP P	S	2P5P PP P PS PDPSCPG	P3PS 3S PSS D CP PCP G						
Ш	HK	S SSPS SP P	S	PP S	4S PPS						
	PL			PP P P CP	PSS						
п	Pr	SSPS SP P	S	SP 4PS PPS PS PD P CS G	P3PS 3SPS P CSPC G						

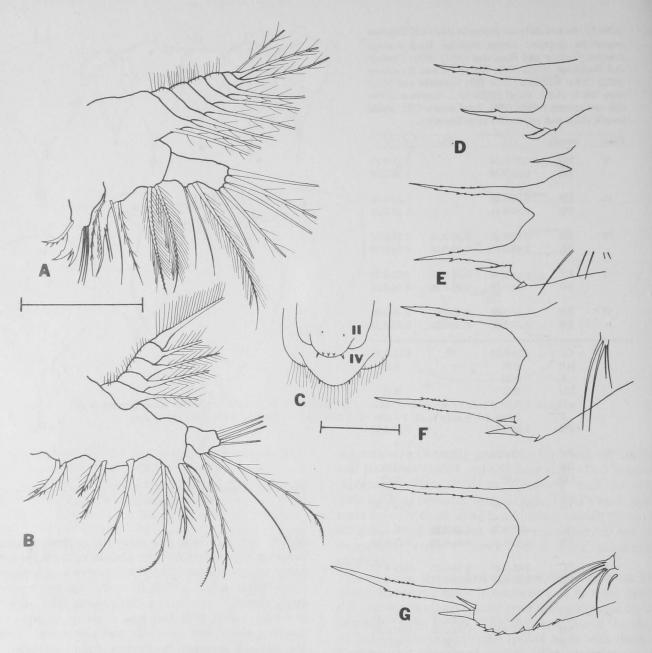


Figure 12.—Balanus improvisus. Antenna of stage IV (A); antennule of stage IV (B); labrum of stages II and IV (C); abdominal process of stage II (D), IV (E), V (F), VI (G). Scale = 0.1 mm.

Balanus improvisus larvae were reared both from North Inlet and Rhode Island adults (Pettaquamscutt Pond) and compared with the excellent descriptions of planktonic larvae from the United Kingdom and Baltic regions (Jones and Crisp 1954).

The shield of B. *improvisus* nauplii (Fig. 11) is without lateral or dorsal spines in all stages. Morphological development at each stage follows the expected sequence (Fig. 4); ps spines are present in stages IV-VI. The fh of stage II nauplii may extend nearly perpendicular to the carapace midline, much as in B. *amphitrite*, but more often are directed slightly forward. In stage III larvae, the fh base extends at a slight forward angle, however, the top curves back. Frontolateral horns in stages IV-VI extend slightly forward similar to B. *eburneus* larvae. Setation follows a normal pattern: the setal formula is nearly identical to that of *B. eburneus* (Table 6). Stage IV nauplii have five An2 endopod terminal setae (Fig. 12A), as opposed to four setae in *B. eburneus*. As noted by Jones and Crisp (1954), the Mn endopod is relatively large (Fig. 12B); the Mn G is well developed. Up to four Mn plumodenticulate setae are present in stages IV-VI.

The AP spination is typical (Fig. 12D-G). One pair of lateral series two spines and a small median spine are present in stages IV and V. The furcal stem is long; the AP and DTS are nearly equal in length in stage IV (Fig. 12E) but the AP is usually longer in stages V and VI (Fig. 12F, G).

The lb (Fig. 12C) is trilobed; the median lobe extends beyond the lateral lobes. In South Carolina nauplii, the median lobe has a distinct pair of lateral teeth; two-four smaller median teeth are also present in earlier naupliar stages. These teeth are less developed in Rhode Island nauplii and are easily overlooked; they are not described for European material (Jones and Crisp 1954).

The larvae of *B. eburneus* and *B. improvisus* are very similar both in size and morphology. Stage II nauplii of these species are nearly the same size in South Carolina during the summer; however, Rhode Island nauplii and winter South Carolina stage II nauplii are noticeably larger (see Table 15). Later stages of B. improvisus tend to be larger but size ranges overlap. In stages II and III, the fh of B. improvisus, particularly the larger cool-water forms, tend to extend perpendicular to the shield; the th of B. eburneus always extend distinctly forward. Balanus improvisus nauplii have distinct teeth on the median labral lobe, this in contrast to B. eburneus and B. amphitrite. In stages IV and VI, B. improvisus nauplii have a broad more rounded cs relative to B. improvisus and B. eburneus, the median AP spine is small or absent, and the AP and DTS are about equal in length. The cyprid of B. improvisus is quite similar in shape to other species of the B. amphitrite complex. Although often the largest sized cyprid in this species complex (Table 16), size ranges overlap and no means for positive identification is presently available.

Balanus subalbidus Henry

A recently described species (Henry 1973), *B. subalbidus* ranges from Massachusetts to Florida on the Atlantic coast (Henry and McLaughlin 1975). It is normally found in intertidal brackish water habitats. No specimens were found in North Inlet, but numerous individuals were collected from intertidal debris at Winyah Bay sites. Identification of samples was provided by Dora Henry.

Larvae of *B. subalbidus* have not been previously reared or described. The following descriptions are based on a small number of larvae successfully reared to stage VI nauplii. The cyprid stage was not obtained nor were additional hatches obtained to verify results.

Balanus subalbidus are generally small and narrow. Early stages average about the same size as *B. amphitrite* nauplii, but late stages approach or surpass sizes observed for *B. eburneus* larvae reared under similar conditions (Table 15).

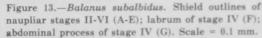
In general appearance, but not size, *B. subalbidus* nauplii resemble those of *Semibalanus balanoides*. The carapace is long and narrow with very short, straight fh (Fig. 13). No lateral or dorsal shield spines are present. The ventral shield spines (stages IV-VI) are long, delicate, and often curved outward.

Setation is virtually identical to that observed for *B. amphitrite* (Table 8). Only the An2 of stage IV varies from *B. amphitrite;* nine plumose setae are on the exopod, but only two postaxial setae are present on the terminal endopod segment (3P:6P-PPSPS:PS:PD: PSCP:G).

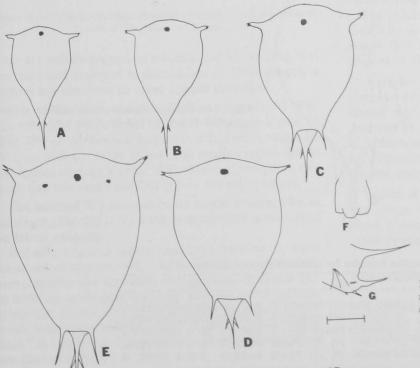
The trilobed lb has a distinctly longer median lobe in all stages (Fig. 13F). No teeth or spines were observed.

The AP is relatively small; the furcal stem is exceptionally short, the maximum observed length being indicated in Figure 13G. In all stages the DTS is distinctly longer than the AP. Abdominal spination is typical; one lateral pair of series two spines but no median spines are present in stages IV and V.

The narrow shield and short fh readily distinguish *B.* subalbidus from all South Carolina species except perhaps *B. amphitrite*. Care must be taken to note the long-







er fh and broader shield of stages II and III of *B. amphitrite* nauplii. Stages IV-VI are readily distinguished on the basis of long ps spines and very short AP of *B. subalbidus* nauplii.

Balanus trigonus Darwin

Balanus trigonus is a warm-water cosmopolitan species which has been reported as far north as North Carolina (Ross et al. 1964). It is subtidal, frequently associated with *B. venustus* and *B. calidus*, and has been reported on numerous hard substrates, including shells, crabs, and sponges (Werner 1967). In North Inlet, *B.* trigonus was found on hermit crab shells, usually single individuals associated with *B. venustus*.

Sandison (1954) briefly described *B. trigonus* nauplii from South African plankton samples. Freiberger and Cologer (1966) reared larvae from Miami, and Barker (1976) reared and described larvae from New Zealand. Present results are based on larvae reared at 25 °C from a single hatch released from a North Inlet adult.

Balanus trigonus nauplii lack dorsal or lateral shield spines in all stages (Fig. 14). Morphological changes at each molt are consistent with the expected pattern (Fig. 4). At stage II, the fh are directed slightly rearward; in subsequent stages the fh extend anteriorly. The shield of stages IV-VI is broad with a moderately arched dorsal surface; the paired ps spines are well-developed. The cyprid is large (see Table 16) with a distinct carapace profile relative to other Carolina species (Fig. 36). The anterior carapace region is wide and well-rounded; a somewhat "teardrop" shape results.

Setation (Table 9) follows the typical balanid pattern although some minor variations were noted. Denticulate

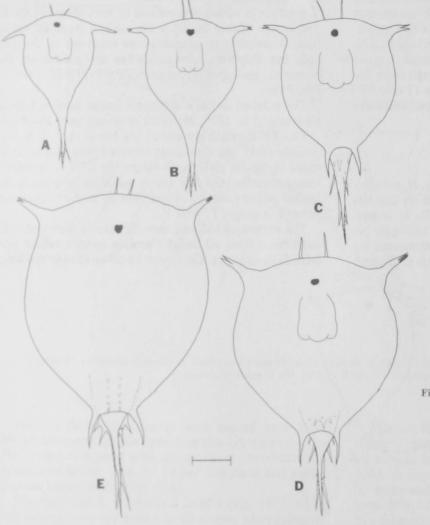
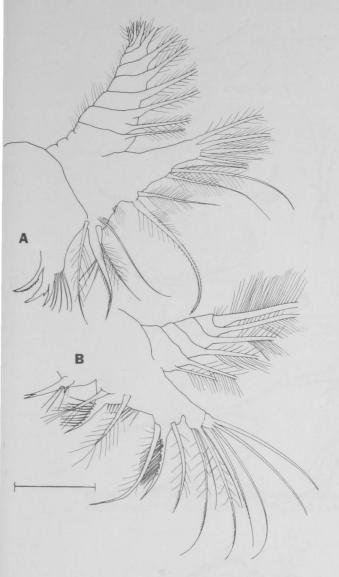


Figure 14.—*Balanus trigonus*. Shield outlines of naupliar stages II-VI (A-E). Scale = 0.1 mm.

Table 9.-Setation formulae for nauplii of Balanus trigonus.

Stage	Anl	An2	Mn							
VI	S P P PSPP SP P PS S	3P 8P 3PSP PSP PD SPCP G	P 5P 3SD SDSD DSCP PCP G							
V	SSPPSPPSPSPSP S	3P 7PS 3PSP PSP PD SPCP G	P 4PS 3SD SDSD DSCP PCP G							
IV	SPPSPPSP P S	3P 5PS 3PSS PSS PD SPCP G	P4P 4S SP P PSCP PCPG							
Ш	S PSPP SP P S	2P5P 3P PS PD PCSG	P3PS3S PSPCPPCG							
II	SSPS SP P S	SP 4PS PPS PS PD SCS G	P3PS3S PSPCPPCG							



igure 15.—Balanus trigonus. Antenna of stage V (A); mandible of stage V (B). Scale = 0.1 mm.

setae are well developed on stages V and VI Mn (Fig. 15); one terminal endopod is denticulate in these stages, a ceature not observed in other species described.

The AP is shorter than the DTS in stages IV-VI (Fig. 16a-c), but is about equal in length for stages V and VI (Fig. 16d-e). Abdominal spination is typical in stages II-IV (Fig. 16A-C); stage IV has one median spine. Series two spines of stage V (Fig. 16D) consist of two pairs; one large and one small median spines are also present.

The trilobed lb has a distinctly longer median lobe in all stages (Fig. 16F). No teeth or denticulation is evident on labral margins.

Balanus trigonus larvae are large relative to most warm-water species; only Chelonibia patula larvae attain a similar size for South Carolina species (Table 15). In addition to the generally large size, the broad yet relatively flat shield with well-developed ps spines distinguish later stage nauplii. Stage II nauplii have "swept back" fh similar to B. amphitrite but B. trigonus larvae are distinctly larger.

Conopea galeata (Linnaeus)

Conopea galeata is a commensal on gorgonians and is restricted to warmer waters. In the western Atlantic it occurs as far north as North Carolina (McDougall 1943). Dead individuals are common on gorgonian branches washed ashore on South Carolina beaches. Several gravid individuals were dredged from tidal creeks at North Inlet, but most gorgonians collected within the inlet are free of commensal cirripeds.

Larvae of *C. galeata* have been reared and described by Molenock and Gomez (1972) using adults collected on the California coast. Present rearing attempts yielded stages I-V; stage VI and the cyprid were not obtained. For the stages obtained, no significant variation was observed relative to Pacific larvae.

All Atlantic larvae were within size ranges cited by Molenock and Gomez (1972). Assuming VI and cyprid stages also fall within these ranges, the mean sizes of C. galeata larvae closely resemble those for B. venustus larvae (see Table 15).

The stage I nauplius (Fig. 17A) shows no distinguishing characteristics. Stage II nauplii are quite distinctive; the shield has numerous short lateral spines (Fig. 17B) and a large median dorsal spine (Fig. 1B). Later stages have two large dorsal spines (Fig. 1F) and numerous lateral spines. Frontolateral horns are long and, in stages III-VI, directed forward. Posterior shield spines are long and curve slightly outward.

The AP spination differs little from the normal balanid pattern. A single pair of series one spines is present in stages II and III, however, additional spines are well developed on the furcal spine (Fig. 17F, H). Series two spines consist of one lateral pair and one median spine in stage IV, two lateral pairs and one median spine in stage V, and six lateral pairs in stage VI. One pair of series three spines are present in stages V and VI.

The trilobed lb (Fig. 17E) has a distinctly longer median lobe. A small spine is present on the median lobe of stages II-V in Atlantic larvae and assumed to be also present in stage VI.

Setation observed agrees closely with the formulae given by Molenock and Gomez (1972). With the exception of only 10 plumose setae on the endopod of stage V An2 and 11 plumose setae on stage VI, the formulae for *C. galeata* are the same as that for *B. amphitrite* (Table 8). Plumodenticulate setae not noted by Molenock and Gomez were observed on the mandibular endopod.

Larvae of C. galeata most closely resemble B. venustus larvae. The large dorsal spine(s) present in all but stage I nauplii readily distinguishes this species from other North Inlet larvae.

Chelonibia patula Ranzani

Chelonibia patula is cosmopolitan in tropical and temperate waters. On the eastern coast it is not normally found much north of the Delaware Bay. Originally reported only from the carapace of crabs (Pilsbry 1916),

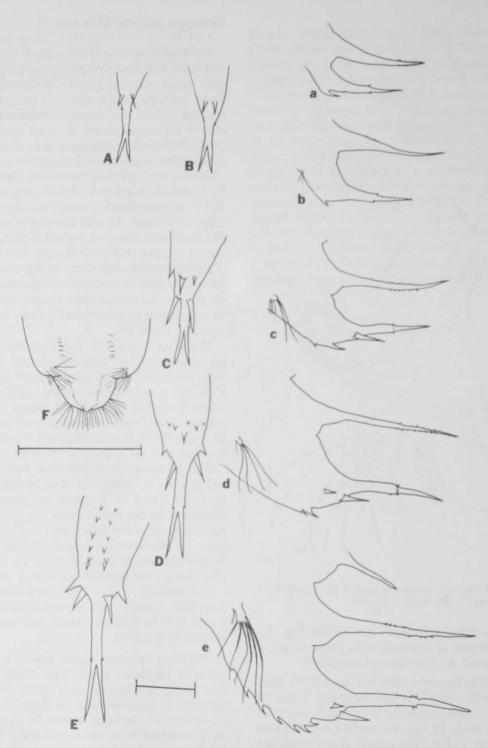
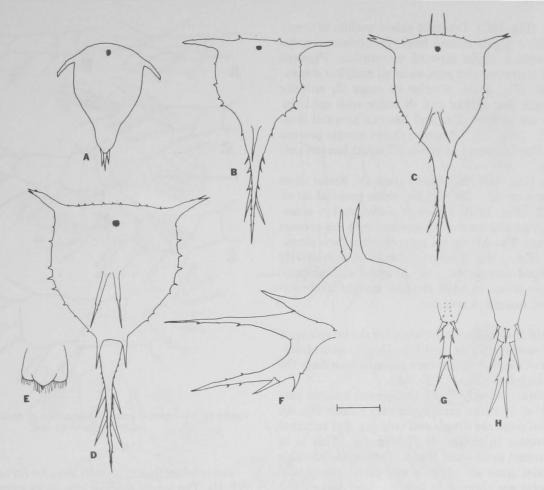


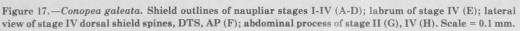
Figure 16.—*Balanus trigonus*. Abdominal process of naupliar stage II (A, a), III (B, b), IV (C, c), V (D, d), VI (E, e); labrum of naupliar stage IV (F). Scales = 0.1 mm.

the species will also settle on shells (Pilsbry 1953). In North Inlet, it is quite common on horseshoe crabs and often found on portunid and spider crabs. Large healthy specimens were also found on hermit crab shells, supporting Pilsbry's later observation.

Coker (1902) reported rearing barnacle larvae from adult acorn barnacles attached to blue crabs, but neither the species nor results were documented further. Lacombe (1973) attempted to rear *C. patula* but obtained only stages I-III. I reared two separate hatches to cyprid stage. As this represents the first complete larval development reported for this genus, a detailed description follows.

Stage I. (Fig. 18B). Rather robust and large with dark brown pigment outlining gut region. Otherwise larvae are typically pear-shaped with folded fh and rudimentary AP.





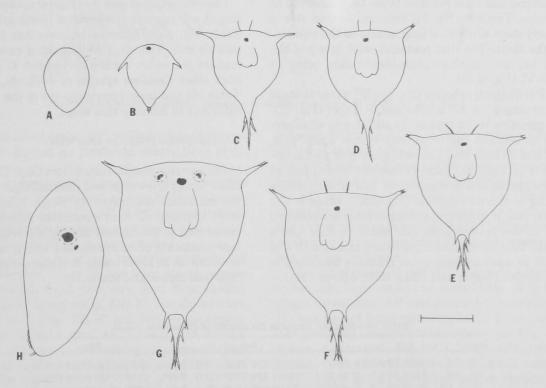


Figure 18.—*Chelonibia patula*. Egg ready to hatch (A); shield outlines of naupliar stages I-VI (B-G); carapace profile of cyprid (H). Scale = 0.1 mm.

Stage II. (Fig. 18C). Cephalic shield outline is nearly circular with a highly arched back. Frontolateral horns are long with a slight forward orientation. Pigment around gut is present and persists in all naupliar stages.

Stage III. (Fig. 18D). Similar to stage II; anterior shield margin less convex and fh wider with split tip. Maxillules are present. The An1 has one preaxial seta.

Stage IV. (Fig. 18E). Posterior shield margin present with short closely spaced ps spines. The An1 has two preaxial setae.

Stage V. (Fig. 18F). Similar to stage IV. Series three spine present on AP. The An1 has three preaxial setae.

Stage VI. (Fig. 18G). Posterior shield region somewhat elongated and narrow. Compound eyes are present after 1-2 days. The AP has six pairs of series two spines.

Cyprid. (Fig. 18H). Large and wide with relatively well-developed compound eyes. Anterior ventral carapace margin tends to have straight margin while anterior dorsal margin is rounded.

The shield in all stages lacks lateral or dorsal spines, is broad and nearly circular, and has a highly arched dorsal surface. A distinct dark brown pigment area rings the gut in all naupliar stages (Fig. 34A).

Setal numbers closely follow the normal balanid pattern (Table 4) however, setal types vary (Table 10). All An1 preaxial setae are simple and only one An1 terminal seta is plumose in stages III-VI (Fig. 19). This is in marked contrast to all other North Inlet species in which some preaxial setae are plumose and three (rarely two) terminal setae are plumose in later naupliar stages. The An2 (Fig. 20) setation is typical, although terminal setae of the endopod have less plumose types than observed in most species. The Mn (Fig. 21) terminal exopod seta is particularly stout with dense long setules on the basal region of the shaft. The first postaxial setal group of the endopod has two distinct plumodenticulate setae in stages IV-VI (Fig. 21D).

The AP is distinctly shorter than the DTS only in stage II. In later stages the AP is subequal or longer (Fig. 22). The AP spination is not typical. In addition to what normally is considered the series one lateral spine pair, stages II and III have an additional spine pair on the furcal stem (Fig. 22A, B). Stage IV has one lateral pair of series two spines and a complex of two small median spines and numerous spinules (Fig. 22C). Stage V has one lateral pair of series two and series three spines and a complex of two lateral pairs and small median spines (Fig. 22D). This latter complex of spines in stages IV and V appears to represent spines not normally described in balanid species (Norris and Crisp 1953; Moyse 1961).

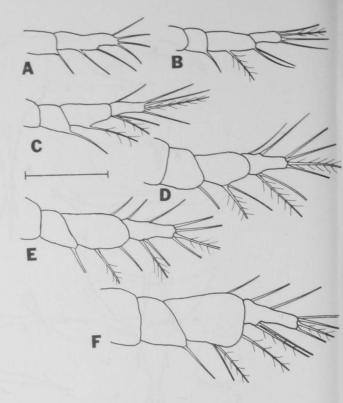


Figure 19.—*Chelonibia patula*. Antennules of naupliar stages I-VI (A-F). Scale = 0.1 mm.

The trilobed lb is typical in form for *Balanus* spp. (Fig. 22F-H). The longer median lobe lacks spines or denticulation in all stages.

Larvae are quite large for tropical species and have the largest average size of described North Inlet species (see Table 15); only *Balanus trigonus* has larvae of comparable size. The large well-rounded carapace and pigmented gut region readily distinguish *C. patula* nauplii from other Carolina species of cirripeds. The size (see Table 16) and large compound eye of the cyprid may be sufficient to identify this stage.

Chthamalus fragilis Darwin

Chthamalus fragilis occurs from Cape Cod south to the West Indies (Newman and Ross 1976), normally on upper intertidal substrates. In North Inlet, C. fragilis is most common on hard substrates (wood, plastic, concrete, etc.) at the highest intertidal levels, but scattered individuals are often intermixed with B. amphitrite and B. eburneus at lower levels. It is also commonly found on Spartina leaves and stalks.

Table 10.-Setation formulae for nauplii of Chelonibia patula.

Stage	age An1						An2		Mn				
VI	SS	S SSPS SP I	PPS	S 3	P9P	2PS SP SF	PPPP	SCP G	P5P	SSSS SD	SD PSCP PCP G		
V	SS	S SSPS SP S	SP	S 2	P8PS	2PS SP SF	PPPP	SCP G	P4PS	SSSS SD	SD PSCP PCP G		
IV	SS	SSPS SP	P	S 2	P 6PS	2PS SS SF	SPPP	SCP G	P4P	SSSS SD	D PSCP PCP G		
III	S	SSPS SP	P	s	P 6P	2PS SF	PPP	SCP G	P 3PS	3S P	SP CPPCPG		
П		SSPS SP	P	S	S 5PS	2PS SF	PPP	SC G	P 3PS	3S P	SP CPPCPG		

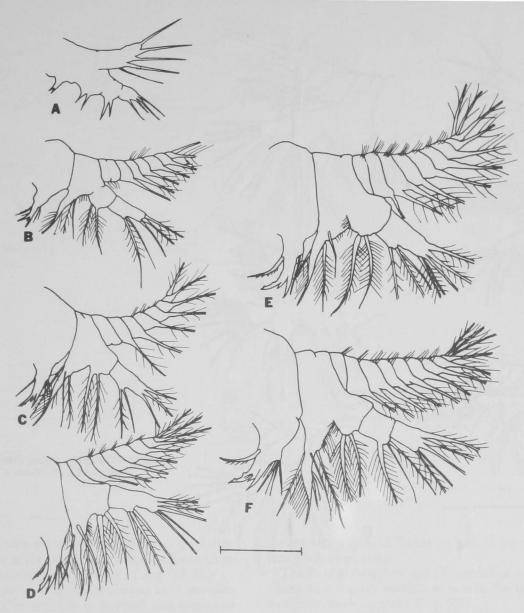


Figure 20.—Chelonibia patula. Antennae of naupliar stages I-VI (A-F). Scale = 0.1 mm.

Larvae of the closely related *C. stellatus* have been decribed (Table 2), but no published descriptions of *C. ragilis* exist.

The nauplii and cyprid of *C. fragilis* are small; average neasurements are the smallest of South Carolina species (see Table 15). Since the AP of later stages usually contracts beneath the posterior carapace margin, total engths for stages IV-VI have been omitted.

Stage I nauplii are small and typically pear-shaped Fig. 23A). However, stage II and later stages have a proad nearly round shield with very short fh somewhat olded under the as margin (Fig. 23G-F). The shield has a highly arched back (Fig. 23b d) and late stages appear 'globular.' No shield spines are present and the ps ppines typical of balanids are lacking. The cyprid (Fig. 23G) is similar to *B. eburneus* or *B. amphitrite* but smaller (see Table 15).

Setal counts of the An1 and Mn follow the balanid pattern (Table 4). The An1 (Fig. 24A) terminal setae vary between SSPS or PSPS in later stages (Table 11), a situation unique to South Carolina species observed. The An2 (Fig. 24B) is unique, having hispid setae, large numbers of postaxial endopod setae (Table 11) and "feathered" or "downy" plumose setae. The Mn (Fig. 24C) cuspidate setae have dense setulation (Fig. 3I) relative to equivalent setae in balanids (Fig. 3H). Plumose setae associated with the cuspidate setae also have dense setules but are not "feathered."

The AP of stages II and III is short with strong furcal spines and large series one spines (Fig. 25A, B). Later stages depart from AP configuration of balanids. In stage IV, one pair of large spines splits from the furcal stem. The resulting configuration appears as four terminal spines or processes (Fig. 25C). In addition, two pairs of lateral spines are evident on the abdominal region. Stage V is similar, but an additional pair of median spines is present between the terminal processes (Fig. 25D). Stage VI (Fig. 25E, F) also has six terminal processes and two

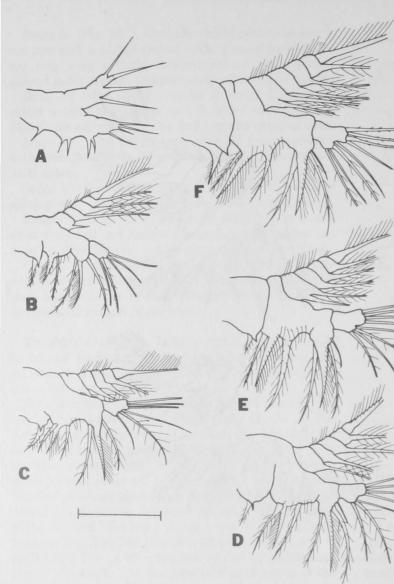


Figure 21.—*Chelonibia patula*. Mandibles of naupliar stages I-VI (A-F). Scale = 0.1 mm.

pairs of lateral spines and, in addition, four pairs of median spines are present. The DTS is longer than the AP in stages II and III (Fig. 23b), subequal in stage IV (Fig. 23d), and very short or rudimentary in stages V and VI (Fig. 26F).

The lb is unilobed. Stages II and III have one pair of larger lateral teeth separated by numerous small denticules (Fig. 26A). The denticles are lost in stage IV (Fig. 26B) and a median porelike protuberance becomes increasingly developed in the late stages (Fig. 26C).

Chthamalus fragilis larvae have features noted as typical for other larvae of the genus: no ps spines; fh folded under the shield; a carapace nearly as broad as long; a unilobed lb; and hispid and feathered setae (Sandison 1967).

The general appearance of the nauplii and small size of the cyprid make larvae of this species quite easy to distinguish in North Inlet, where no other chthamalid species occur.

Octolasmis muelleri (Coker)

Octolasmis muelleri is a small pedunculate barnacle found attached to the gills of the blue crab, Callinectes sapidus, and other decapod hosts (Walker 1974b). First described from Beaufort, N.C., by Coker (1902), O. muelleri is perhaps synonymous to the cosmopolitan Octolasmis lowei (Nilsson-Cantell 1927; Causey 1961) or a local race or subspecies (Pilsbry 1953) of a shallow-water O. lowei-series (Table 12). In the western Atlantic its known range extends southward from the Chesapeake Bay through the Gulf of Mexico and Caribbean Sea to Brazil (Lang 1976).

The complete larval development of this species has been recently described using larvae released from North Inlet adults (Lang 1976). An additional octolasmid species, Octolasmis forrestii (Stebbing), has subsequently been obtained from the gills of a spiny lobster captured in Belize, Central America; released larvae were suc-

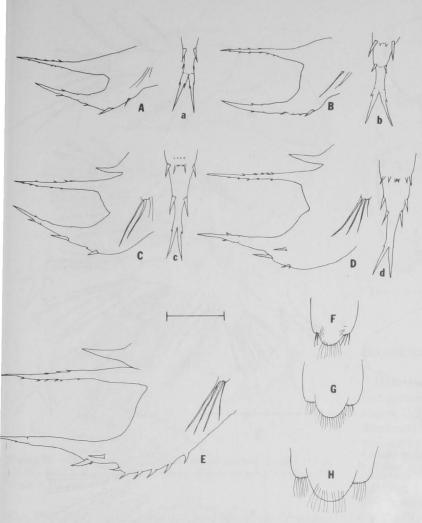


Figure 22.—*Chelonibia patula*. Abdominal process of stage II (A, a), III (B, b), IV (C, c), V (D, d), VI (E); labrum of stage II (F), IV (G), VI (H). Scale = 0.1 mm.

cessfully reared through stage VI nauplius. A brief comparative account of the larval development of both Octoasmis species follows; for details see Lang (1976).

Larvae of *O. forrestii* are quite similar to *O. muelleri* Figs. 27, 28). The nauplius cs is small and triangular and develops small blunt lateral spines in later stages. The AP and DTS are considerably longer than the shield, and the fh are also quite long. In both species development of the ps border is delayed until stage V.

The appendages of octolasmid nauplii are distinctive. The An1 and An2 are elongate relative to balanomorph hauplii while the Mn is small with a poorly developed exopod (see Figs. 33A, 34C). Setation of *O. forrestii* hauplii differ from those of *O. muelleri* (Table 13) only at tage IV (Fig. 29). Bristled setae (Fig. 3M) are present on he An1 (Fig. 29A); development of setae at each molt, however, follows a pattern similar to balanomorph hauplii. The An2 exopod setae are long and delicate; unike balanomorph species, setules are restricted to one ide of the shaft for these setae. The Mn (Fig. 29C) shows ittle increase in size during molts; exopod setation Table 13) is significantly reduced in later stage nauplii elative to all other described planktotrophic cirriped hauplii.

The AP and DTS of octolasmid nauplii are extremely ong, a feature also seen in *Lepas* nauplii (see Fig. 30).

Unlike *Lepas* nauplii, larvae of both *Octolasmis* species lack abdominal spines.

The lb of *O. muelleri* and *O. forrestii* is unilobed and tapers to a median porelike structure. No teeth or denticulation were observed (Fig. 29D).

Development of O. forrestii nauplii incorporates the same unique features described for O. muelleri (Lang 1976). Morphology and naupliar size of these two species varies little; identification to species from field samples would be virtually impossible in areas where numerous Octolasmis species occur. In coastal Carolina waters, however, O. muelleri is the only octolasmid species commonly present. Only Lepas nauplii are similar in appearance; size and lb morphology easily distinguish these larvae. Although the nauplii of O. muelleri are distinctive, the cyprid (see Fig. 36C) closely resembles Balanus amphitrite-complex cyprids. Identification is possible based on the symmetric carapace profile of O. muelleri cyprids as opposed to the enlarged anterior region and tapered posterior region common to Balanus species.

Lepas spp.

Five species of *Lepas* are commonly found in the western Atlantic (Zullo 1963). All are open water neustonic forms whose occurrence in coastal waters is usually

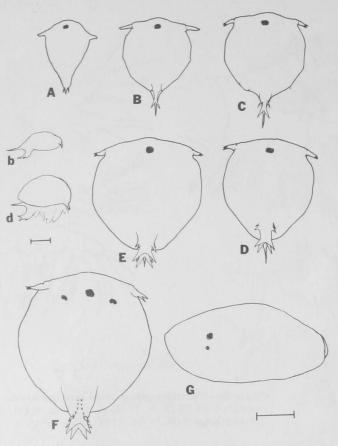


Figure 23.—*Chthamalus fragilis.* Shield outlines of naupliar stages I-VI (A-F); lateral profile of stage II (b), IV (d); carapace outline of cyprid (G). Scales = 0.1 mm.

restricted to introduction by ships or floating debris directed shoreward by storms. Collections on South Carolina beaches following storms have produced *Lepas* anatifera on driftwood and *L. anserifera*, *L. pectinata*, and *L. fascicularis* on sargassum. Lepas hilli, although not observed in present collections, should also occur on occasion.

Although breeding populations of Lepas are not commonly found in coastal waters, circumstance introduction of gravid adults may result in local release of Lepas larvae. The complete larval development of L. fascicularis has been reconstructed from plankton samples (Willemoes-Suhm 1876; Bainbridge and Roskell 1966). John Moyse reared nauplii of L. pectinata and L. anatifera (pers. commun.) but larvae remain undescribed. In present studies up to stage V nauplii of L. pectinata and stage III nauplii of L. anserifera have been reared from gravid adults washed ashore. Larvae obtained are quite similar to those described for L. fascicularis. Staging of

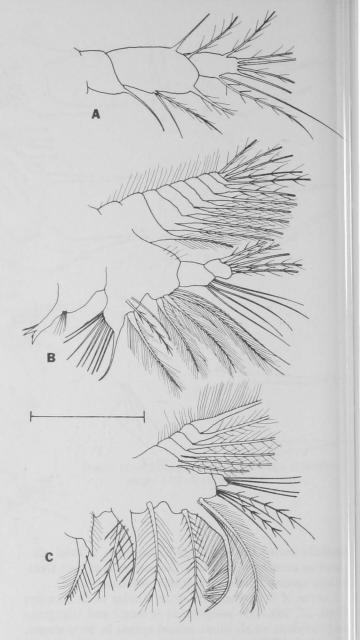


Figure 24.—*Chthamalus fragilis.* Antennule of stage IV (A); antenna of stage IV (B); mandible of stage IV (C). Scale = 0.1 mm.

Lepas larvae is not difficult (see Bainbridge and Roskell 1966); however, identification of nauplii to species must await further descriptions of Lepas larvae. Using L. pectinata as an example, general features of Lepas nauplii are outlined below.

Lepas nauplii have very long fh, a DTS, and an AP (Fig. 30A-C). The shield of stage II nauplii is plain (Fig.

Table 11Setation formulae for nau	plii of Chthamalus fragilis.
-----------------------------------	------------------------------

Stage	Ant	1						An	2				Mn	1	
VI	SPPPSPP	SP	PPS	SS	4P 8P	PPSI	PP	PSSSS	SFFF	SPFH G	P 5P	SSSS SPS	SP P	SCP	PPC G
V	SPPPSPP	SP	SP	S	4P 7P	PPSI	PP	PSSS	SFFF	SPFH G	P 4PS	4S SPS	SP P	SCP	PPC G
IV	S P PSPP ^s	SP	Р	S	3P 6P	PPSI	PS	PSS	SFF	SPFH G	P4P	4S SP	PP	SCP	PPC G
Ш	S PSPS ^r	SP	Р	S	2P 5P	PP 1	Р	PSS	FF	SFH G	P 3PS	4S SP	Р	CP	PPC G
Ϊ	SSPS	SS	Р	S	SP 4PS	PP	S	SS	FF	SFH G	P 3PS	3S SP	P	CP	PC G

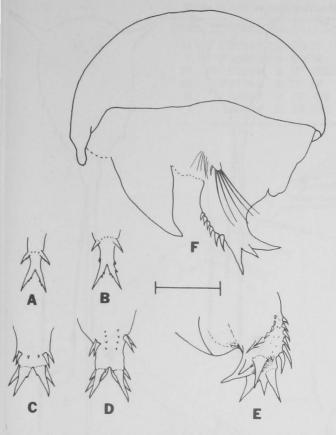


Figure 25.—*Chthamalus fragilis.* Abdominal process of stage II (A), III (B), IV (C), V (D), VI (E); lateral profile of stage VI nauplius (F). Scale = 0.1 mm.

30A, B). Later stages have dorsal and lateral shield spines and often appear quite "ornate" (Fig. 30C). The densely spinose AP is highly arched in early stage nauplii (Fig. 30A, B); abdominal spines are present (Fig. 30D, E) and may be used to stage nauplii (Bainbridge and Roskell 1966). The lb is broad edged with one or more pair of teeth (Fig. 30F). Setation includes bristled setae on the An1 (Fig. 30G) and feathered setae on the An2 (Fig. 30H). The Mn is well developed with notably long postaxial endopod setae (Fig. 30I). A Figure 2 of stage mm.

Figure 26.—*Chthamalus fragilis*. Labrum of stage III (A), IV (B), VI (C). Scale = 0.1 mm.

Nauplius SC

Examination of plankton samples taken 2 to 35 mi off Georgetown Harbor, S.C., during October 1976, yielded stages II-VI of an undescribed cirriped larva. The predominant barnacle larvae present in all samples examined have been designated "nauplius SC."

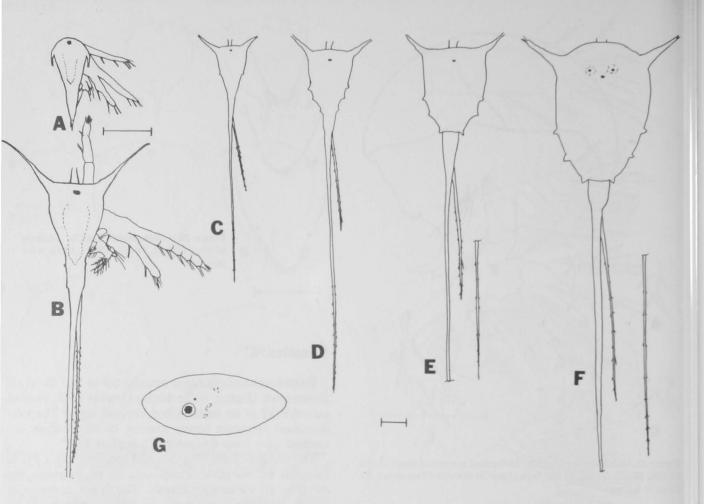
The elongate form (Fig. 31) and size (see Table 15) of nauplius SC resembles *Octolasmis* larvae, however, the AP (Fig. 31) varies significantly. The fh are moderate in length and directed rearward. Basic morphological changes at each molt closely follow the expected balanid pattern.

Setation (Table 14) is unique. The An1 (Fig. 32A) is typical and shows a normal setation progression at each molt. The An2 (Fig. 32B) endopod has feathered setae and large numbers of setae in later stage nauplii. The Mn (Fig. 32C) is well developed with typical setation patterns.

The DTS is long in all naupliar stages, a feature also seen in *Lepas*, *Octolasmis*, and *Verruca* (LeReste 1965)

Synonyms of Octolasmis lowei Darwin-Nils	sson-Cantell (1927)
Dichelaspis lowei Darwin, 1851	Madeira
Dichelaspis darwini Filippi, 1861	Mediterranean
Dichelaspis aymonini Lesson, 1874	Japan
Dichelaspis neptuni Mac Donald, 1869	Australia
Dichelaspis sinuata Aurivillius, 1894	Java Sea
Dichelaspis trigona Aurivillius, 1894	Java Sea
Dichelaspis mulleri Coker, 1902	North Carolina
Dichelaspis vaillantii Gruvel, 1902	Suez
Octolasmis geryonophila Pilsbry, 1907	Atlantic
Subsequent Modifications and A	dditions
O. aymonini-reinstated as species	Hiro (1937)
O. brevis-Pearse, 1951 added as synonyms	Newman (1961

O. aymonini-reinstated as species	Hiro (1937)
O. brevis-Pearse, 1951 added as synonyms	Newman (1961)
O. uncus-Pearse, 1951	
O. neptuni-reinstated as species	Newman (1961)
O. geryonophila-changed to synonym of O. aymonin	Newman (1967)





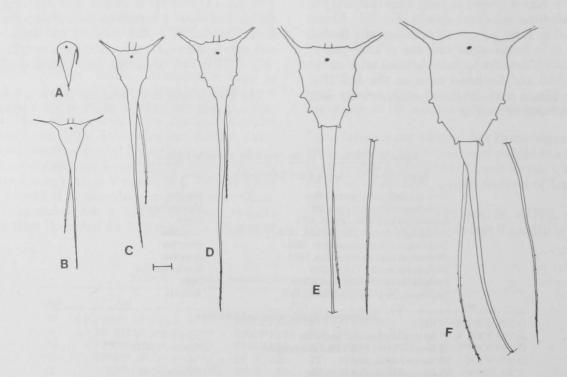


Figure 28.-Octolasmis forrestii. Shield outlines of naupliar stages I-VI (A-F). Scale = 0.1 mm.

Table 13.-Setation formulae for nauplii of Octolasmis muelleri.

Stage			An1						Mn									
VI	SP	Р	SBS	SB	P	В	S3P	7P	4P	2P	s	SS	СG	SSS	3S	CPP	PPP	G
V	SP	P	SBS	SB	S	B	S2P	7P	4P	2P	S	SS	CG	SSS	3S	CPP	PPP	G
		Р	SBS	SB		B	2P	5P2S	3PS	PS	S	SS	CG	SS	35	CPP	PPP	G
Ш		P	SPSS	S B		В	2P	5P	3P	P	S	S	CG	SS	3S	CPP	PPP	G
Π			SPSS	S B		В	SP	4PS	2PS	S	S	S	CG	SS	35	CPP	PP	?
Ι			SSS	SS		s	SS	SSS	3S	S	s		G	SS	SS	SSS	SS	

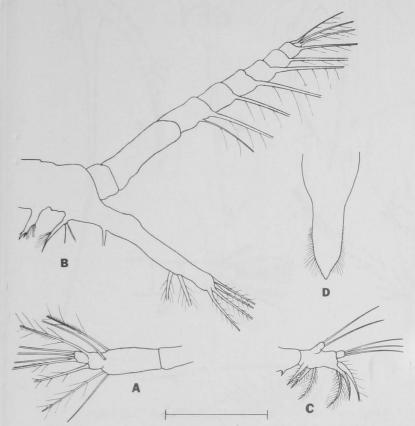


Figure 29.—Octolasmis forrestii. Antennule of stage IV (A); antenna of stage IV (B); mandible of stage IV (C); labrum of stage IV (D). Scale = 0.1 mm.

nauplii. The AP, however, is unique; a narrow stem is absent as the basal region splits directly into the furcal processes (Fig. 31). Abdominal spination is restricted to one large median spine in stages II-V (Fig. 31A-D) and six smaller paired spines in stage VI (Fig. 31E, e).

The lb (Fig. 31) is unilobed and tapers to a blunt denticulate tip in all stages.

Larvae of this unknown species were not found within North Inlet or Winyah Bay but were common (in October) in nearshore waters. The general body form and unique AP structure of this nauplius readily distinguishes it; however, larvae of this species do not closely match larvae of any presently described family (Table 2). Possible affinities of these nauplii are discussed later.

Hansen (1899) described 10 "species" of cirriped nauplii from material collected by the Plankton-Expedition. Based on carapace, DTS, and labrum morphology, Hansen's "nauplius" may represent stage III and IV of nauplius SC or at least a closely related species. Similarly "nauplius α " probably represents a stage VI Balanus trigonus nauplii and "nauplius β " appears to be stage IV and VI Balanus amphitrite nauplii. However, since Hansen did not describe appendages and other naupliar detail, comparisons with present descriptions are tenuous.

KEYS TO THE BARNACLE LARVAE OF THE CAROLINAS

Assigning Stages

Based on reared and planktonic material, it is possible to construct a key to the predominant barnacle nauplii of the Carolina coastal waters. The key is limited to naupliar stages II-VI: stage I nauplii show little morphological variation and are rarely encountered in plankton samples while many cyprids (see page 36) cannot be reliably identified to species. A two-step procedure is followed. Since each naupliar stage often has its own set of morphological features and size ranges, nauplii must first be accurately "staged." Different keys for each stage or group of stages are then used to identify the species of the nauplius.

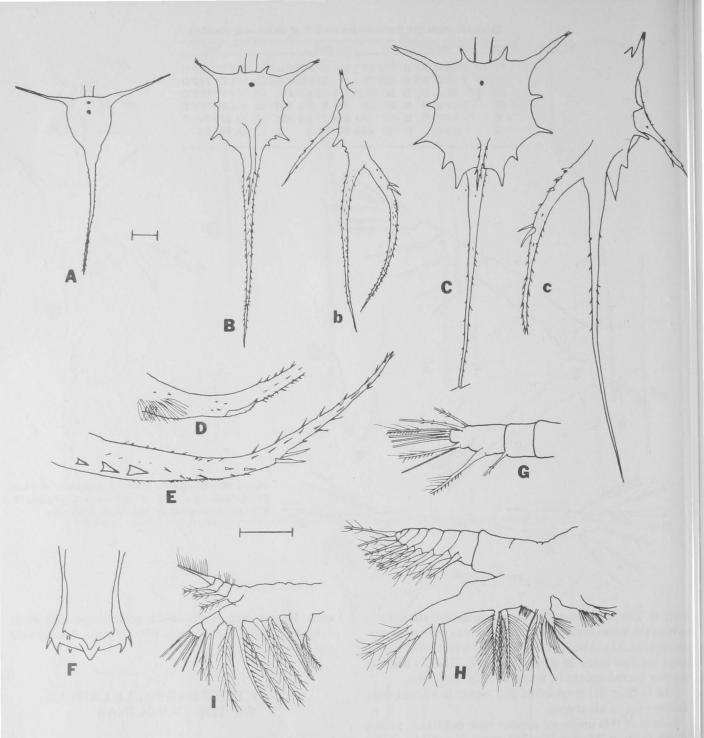


Figure 30.—Lepas pectinata. Shield outline of naupliar stage II (A); shield outline (B) and lateral profile (b) of stage III; shield outline (C) and lateral profile (c) of stage IV; abdominal spines of stage II (D) and stage IV (E); labrum of stages II and IV (F); antennule of stage IV (G); antenna of stage IV (H); mandible of stage IV (I). Scales = 0.1 mm.

Morphological features cited below for assigning stages of barnacle nauplii are shown in Figure 4. Abdominal process characters normally apply only to balanomorph larvae; other features are valid for all larvae except *Octolasmis.* In this case only the setation of the An1 is valid. See Figures 1 and 4 for a complete list of terms and abbreviations.

1a.	Frontolateral horns folded back, AP rudi-	
	mentaryStage	eΙ
1b.	Frontolateral horns extended, AP well de-	
	veloped	2
2a.	Posterior shield margin absent	3
2b.	Posterior shield margin present	4

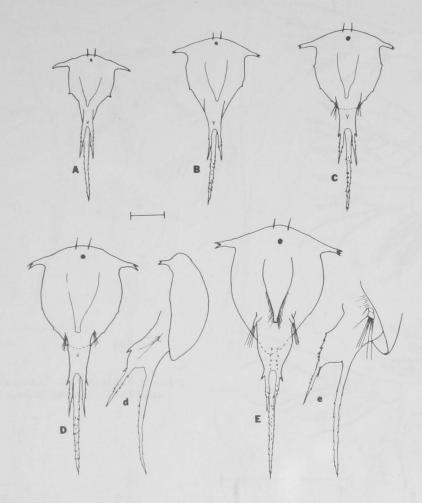


Figure 31.—"Nauplius SC." Shield outlines of naupliar stages II-VI (A-E) and lateral profiles of stages V (d) and VI (e). Scale = 0.1 mm.

	Table	14	-Setation	formulae	for	nauplii	Υ.
--	-------	----	-----------	----------	-----	---------	----

Stage	Stage An1							An2										Mn						
VI	SPPPS	PP	PP	P PS	SP	4P 8P	PPS	SPPS	PPPS	SFFF	PF	SCG	P5P	PPS	SPPS	PSP	S SPCI	PPF	G					
V	SPPPS	PP	SP	SP	Р	3P 8P	PPS	SPP	PPP	SFFF	PF	SCG	P4PS	PPS	SPP	PSP	S SPCI	PPF	G					
IV	SPPS	PP	SP	Р	Р	2P 7P	PP	SPS	SPP	SFF	PF	SCG	P4P	SPS	SPS	PSP	SPCI	PPF	G					
III	SPS	PP	SP	Р	Р	2P 5P	PP	Р	PP	FF	PF	SCG	P 3PS	SP	SP	P P	PCI	PPF	G					
П	SS	PS	SP	S	S	2S4PS	PP	S	SP	FF	SF	СG	P 3PS	SS	S	S P	PCI	PPP	G					

- 5a. An1 with two preaxial setae, AP with series two spine pair Stage IV
- 5b. An1 with three preaxial setae, AP with series two and series three spine pairs Stage V

Species Identification of Nauplii

Stage II nauplii are in many instances the most commonly encountered larval stage in plankton samples (Lang see footnote 3) and for this reason complete figures

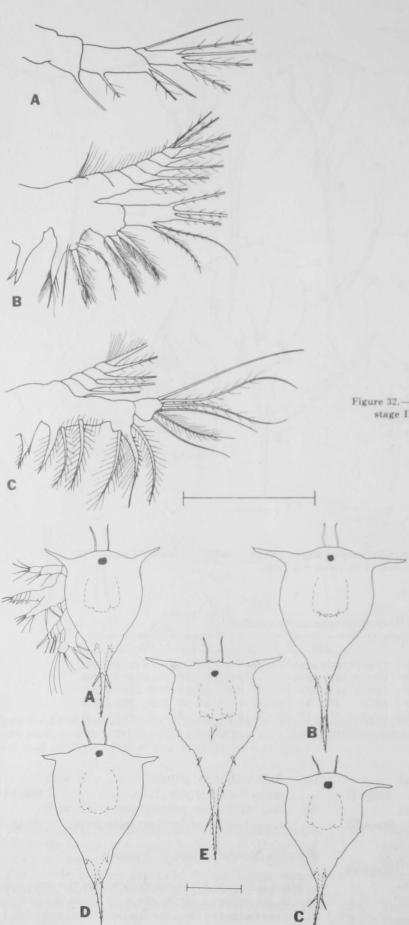


Figure 32.—"Nauplius SC." Antennule of stage III (A); antenna of stage III (B); mandible of stage III (C). Scale = 0.1 mm.

> Figure 33.—Stage II nauplii of Balanus amphitritecomplex species common in Carolina waters: Balanus eburneus (A); B. improvisus (B); B. amphitrite amphitrite (C); B. subalbidus (D); B. venustus (E). Scale = 0.1 mm.

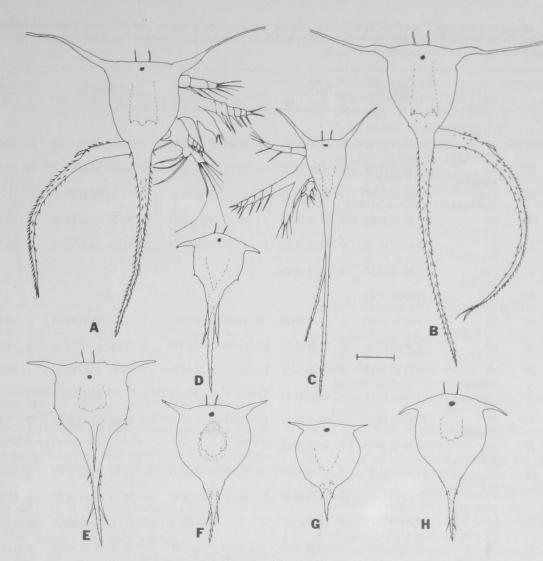


Figure 34.—Stage II nauplii of barnacle species found in Carolina waters: Lepas pectinata (A); Lepas anserifera (B); Chelonibia patula (C); "nauplius SC" (D); Conopea galeata (E); Chelonibia patula (F); Chthamalus fragilis (G); Balanus trigonus (H). Scale = 0.1 mm.

for common stage II nauplii are provided (Figs. 33, 34) and the stage II key should be studied prior to use of later stage keys.

The present keys should account for most barnacle larvae found in shallow-water regions from Georgia to North Carolina. As evident by "nauplius SC," some undescribed nauplii can be expected, particularly in offshore samples. Difficulties in species identification of nauplii, for the most part, is limited to *Balanus amphitrite*-complex species (Fig. 33). Early stages of *B. eburneus*, *B. improvisus*, and *B. amphitrite* are particularly difficult to distinguish and may be easily confused.

The size of nauplii, in many instances, provides rapid clues to both stage and identity of the specimen, however, caution should be exercised. Laboratory rearing clearly demonstrates that significant size differences in larvae may be induced by the temperature of egg incubation and/or larval rearing (Lang see footnote 3). Sizes of nauplii (Table 15) and cyprid (Table 16) show that larvae developing in warmer water tend to be smaller than larvae of the same species developing in cooler water. Summer and winter stage II nauplii of *B. improvisus* from North Inlet plankton samples and summer larvae from Rhode Island show considerable size variation; both seasonal and geographical size variation should be expected.

Key to Stage II Nauplii of the Carolinas

1a.	Labrum unilobed (Fig. 26) 2
1b.	Labrum trilobed 5
2a.	Shield rounded, DTS shorter than
	shield length (Fig. 34G) Chthamalus fragilis
2b.	Shield triangular, DTS longer than shield length
	Labrum with flat toothed edge (Fig.
	35a, 34A, B) Lepas spp.
3h	Labrum tanered to blunt tin (Fig. 35A) 4

Table 15.—Size ranges of barnacle nauplii obtained by laboratory rearing and plankton samples. Measurements represent millimeters/100 (38 = 0.38 mm); n = number measured, TL = total length, SL = shield length, W = width; SC = North Inlet, South Carolina; RI = Narragansett Bay, Rhode Island. See Materials and Methods for diet symbols.

		Diet	Stage	II		Stage III		Sta	age IV			St	age V			Sta	ge VI	
Species	Source	Temp (°C)	n TL	W	n	TL W	n	TW	SL	W	n	TL	SL	W	n	TL	SL	W
Delement		TET/MON																
Balanus amphitrite	SC	25	29 28-34 1	2-16	27	31-36 16-20	13,	33-40	24-30	17-23	12	40-47	28-25	24-28	10	47-57	34-39	27-3
Balanus		TET/MON																
eburneus	SC	25 Plankton	10 32-36 1	6-18	10	36-41 18-23	10	42-45	30-33	23-25	15	46-57	33-44	26-32	15	57-62	39-46	32-3
Balanus	SC	July TET/3H	8 31-33 1	5-17	7	37-41 20-22	10		28-32	22-24	7		37-40	28-30	1		42	4(
improvisus	SC	25	15 28-31 1	3-14	10	32-38 16-19	10	41-46	29-32	24-27	10	52-62	37-41	32-35	10	65-72	48-52	40-43
	RI	TET/MON 20	10 34-37 1	6-18	10	37-43 19-21	10	41-46	29-32	25-28	10	51-60	39-43	32-36	10	63-76	52-58	37-4
	SC	Plankton Jan. Plankton	10 35-38 1	16-18	2	38-41 19-20												
Balanus	RI	Nov. TET/MON	15 35-43	17-20														
subalbidus Balanus	SC	25 TET/MON	6 30-31 3	4-15	5	32-35 18-19	6	36-45	29-31	20-23	7	48-51	36-40	24-30	6	56-64	44-48	33-3
trigonus Balanus	SC	25 TET/MON	5 38-40	17-18	10	44-48 23-24	11	51-56	31-36	28-32	2	61-65	41-42	36-38	10	74-81	51-57	43-5
venustus	SC	25 Plankton	15 37-40	17-19	10	41-45 19-22	10	44-50	29-33	23-27	10	54-64	38-43	29-34	7	68-76	44-51	34-3
	SC	July TET/SKEL	4 38-40	17-18	4	43-47 21-23	2		35-40	29-31	3		40-41	34-35	2		50-52	41-4
	RI	20 Plankton	10 34-39	16-18	10	40-46 20-23	12	41-53	32-35	23-28	13	51-64	38-43	28-35	10	72-80	49-57	37-43
01 J 11	RI	Oct.	10 39-44	18-20	5	44-48 21-23												
Chelonibia	SC	3H/MON 25	10 42-44 5	11 00	10	45-49 25-28	10	52-60	25 42	00.07	12	63-67	10 51	20.40	6	73-81	54.01	10 5
patula Conopea	~~~	25 lenoch and	10 42-44	21-20	10	40-49 20-20	10	52-60	30-43	32-31	12	03-07	40-04	39-42	0	/3-81	04-01	42-00
galeata Chthamalus	1	mez 1972) TET/MON	77 32-44	16-20	53	40-50 20-26	57	48-58	24-34	22-31	45	56-74	34-44	30-37	33	60-86	42-58	36-4
fragilis	SC	25	10 24-26	17-18	10	26-30 17-20	10		24-25	23-24	8		30-31	26-29	5		44-47	19-2-
Octolasmis muelleri	SC	TET/MON 27	8 79-85	10-77	10	92-111 12-14	9	118-134		16-18	6	167-182	2 32-36	23-27	9	254-278	52-55	36-3
Nauplius SC	SC	Plankton	0 10	10	0	10 51 15 10	10	54.50	00.05	10.10	0	01.05	00.00	00.07		00.54	00.00	00.0
		Oct.	2 42	12	8	48-51 15-16	10	54-58	23-25	18-19	6	61-67	26-30	22-24	5	66-74	36-38	26-28

Table 16.—Size of barnacle cyprids reared in the laboratory: SC = North Inlet, South Carolina, RI = Narragansett, Rhode Island; n = number measured. See Materials and Methods for diet abbreviations.

and a maintain a sea	-	1 1412 1 15			Width Length (microns)		
Species	Source	Diet-Temp.	°C	n	$x\pm sd$	$x\pm sd$	
Balanus amphitrite	SC	TET/MON	20	32	239 ± 17	499±14	
	SC	TET/MON	25	38	214 ± 17	477 ± 22	
Balanus eburneus	SC	TET/MON	20	12	247 ± 08	547 ± 16	
	SC	TET/MON	25	14	242 ± 11	528 ± 22	
Balanus improvisus	SC	TET/MON	25	5	267 ± 19	551 ± 26	
	RI	TET/MON	20	10	257 ± 24	573 ± 16	
Balanus trigonus	SC	TET/MON	25	7	264 ± 19	570 ± 27	
Balanus venustus	SC	TET/MON	25	6	235 ± 10	545 ± 08	
	RI	TET/MON	20	16	243 ± 16	572 ± 34	
Chelonibia patula	SC	TET/MON	25	10	262 ± 05	648 ± 30	
Chthamalus fragilis	SC	TET/MON	25	25	217 ± 22	456 ± 25	
Octolasmis mueller	i SC	TET/MON	27	10	223 ± 21	572 ± 25	

- 4a. Abdominal process long, furcal lobes absent or poorly developed (Fig. 35B, 34C) Octolasmis muelleri

5a. 5b.	
	Dorsal shield spine long (Fig. 34E) C. galeata Dorsal shield spine short (Fig. 33E)
7a.	Frontolateral horn tips directed distinctly
	forward (Fig. 35C) 8
7b.	Frontolateral horn tips perpendicular to shield median axis or directed rearward
	(Fig. 35c) 10
8a.	
	shield (Fig. 34F)C. patula
8h	Larva less than $200\mu m$ wide, shield ellip-
00.	tical
9a.	Labrum with distinct teeth on median
ou.	lobe (Fig. 33B) B. improvisus (summer)
9h	Labrum without distinct teeth on median
00.	lobe (Fig. 33A) B. eburneus
10a.	
10a.	33D)B. subalbidus
101	
10b.	Frontolateral horns normal 11

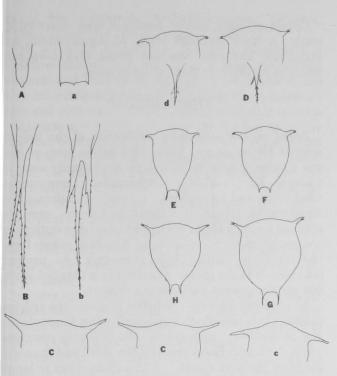


Figure 35.—Morphological features of Carolina barnacle nauplii: labrum of Octolasmis (A) and Lepas (a); AP and DTS of Octolasmis (B) and "nauplius SC" (b); forward orientation (C) and perpendicular orientation (c) of frontolateral horns; frontolateral horns and AP-DTS configuration of Balanus subalbidus (D) and B. a. amphitrite (d); stage IV carapace outlines of B. subalbidus (E), B. amphitrite (F), B. eburneus (H), and B. trigonus (G). (See naupliar keys for details.)

11a.	Larva less than 340 μ m wide, lateral shield margin somewhat straight with one pair of small rounded spines (Fig. 33c)B. amphitrite
11b.	
12a.	
12h	Frontolateral horns curved slightly poste-
120.	riorly, lb median lobe without teeth (Fig.
	34H)B. trigonus
1	Key to Stage III Nauplii of the Carolinas
1a.	Labrum unilobed as in stage II key
	Labrum trilobed
	Shield with paired dorsal spines
	Shield without dorsal spines 7
6a.	Dorsal shield spines long, approximate
	length of fhC. galeata
6b.	Dorsal shield spines very short B. venustus
	Shield wide (over 250 μ m) and roundC. patula
	Shield narrow (less than 250 µm) 8
80	Frontolateral horns directed perpendic-

Key to Stages IV-V Nauplii of the Carolinas

1a.	Labrum unilobedas in stage II key
1b.	
5a.	
5b.	
6a.	
	lateral spines C. galeata
6b.	
	spinulose shield margins B. venustus
7a.	Shield nearly as wide as long, PS spines
	short, An1 with SPPS terminal setae C. patula
7b.	Shield longer than wide, An1 with PSPP
	terminal setae 8
8a.	Frontolateral horn tips perpendicular or
	directed rearward 9
8b.	Frontolateral horn tips directed forward 10
9a.	Frontal horns short, PS spines long, AP
	less than one-half length of DTS (Fig.
	35E)B. subalbidus
9b.	Frontolateral horns short to moderate, PS
	spines short, AP one-half length of DTS
	(Fig. 35F)B. amphitrite
10a.	Abdominal process subequal or longer
	than DTSB. improvisus
10b.	Abdominal process shorter than DTS 11
11a.	1 0, 0
	five median spines on AP (Fig. 35G). B. trigonus
11b.	
	stage V with three median AP spines (Fig.
	35H) B. eburneus

Key to Stage VI Nauplii of the Carolinas

1a.	Labrum unilobed as in stage II key
1b.	Labrum trilobed 5
5a.	Shield with two dorsal spines C. galeata
5b.	Shield without dorsal spines 6
6a.	Abdominal process subequal or longer
	than DTS 7
6b	Abdominal process shorter than DTS

7a.		
7b.	Antennules with PSPP terminal setae 9]
8a.	Posterior shield spines longer than fh	,
	B. subalbidus	1
8b.	Posterior shield spines equal or shorter in	
	length than the fh 10	
9a.	Shield length greater than 560 μ m B. trigonus	
9b.	Shield length less than 560 μ m B. improvisus	
10a.	Antennae with 11 setae on exopod B. venustus	
10b.	Antennae with 12 setae on exopod 11	,
11a.	Shield length generally greater than 400	3
	μ m, fh tip extends straight B. eburneus	
11b.	Shield length generally less than 400 μ m,	

fh tip bent rearwardB. amphitrite

Cyprids

Cyprid larvae are very similar in most barnacle species. Size (Table 16) and even length to width ratios of the carapace (Fig. 36E, F) vary with rearing conditions (Lang see footnote 3). Present studies have failed to find reliable means to identify *B. amphitrite-*complex cyprids to species. Although *Chthamalus fragilis* cyprids (Fig. 36B) tend to be smaller, even this species may be confused with cyprids of *B. amphitrite.*

Octolasmis cyprids (Fig. 36C) are "bean"-shaped with little size difference in anterior and posterior carapace regions; fresh specimens have a distinct bright orange pigment (Lang 1976).

Chelonibia patula cyprids (Fig. 36A) are the largest larvae of balanomorph species in the Carolinas (Table 16). The large compound eye is distinctive.

Balanus trigonus (Fig. 36D) are also large but have a small compound eye. The carapace is "teardrop" in shape with well-rounded margins.

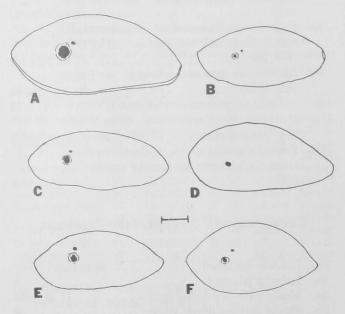


Figure 36.—Cyprids of South Carolina: Chelonibia patula (A); Chthamalus fragilis (B); Octolasmis muelleri (C); Balanus trigonus (D); Balanus amphitrite reared at 30°C (E); B. amphitrite reared at 20°C (F). Scale = 0.1 mm.

Cyprid of other species have not been observed directly. A more thorough study of pigmentation, size variations, and fine carapace detail may eventually result in methods to identify all cyprids.

DISCUSSION

Based on the proposed classification of the Balanomorpha (Newman and Ross 1976), larvae from at least one species of each balanomorph superfamily were examined: Chthamaloida, Chthamalus; Coronulaidea, Chelonibia; and Balanoidea, Conopea and Balanus. Two lepadomorph genera, Octolasmis and Lepas, were also studied. As the number of cirriped larval descriptions increases, it may be possible to correlate many larval characteristics with adult taxonomy. At present, information is too sparse to undertake a detailed study, but certain general patterns are evident.

As observed by many previous authors, the trilobed naupliar lb is specific to the superfamilies Coronulaidea and Balanoidea. These groups were originally combined under the family Balanidea (Pilsbry 1916) and the use of the term "balanid nauplii" in this study refers to larvae from either superfamily. A unilobed lb occurs in larvae from the remaining barnacle groups—the balanomorph superfamily, Chthamaloida, and all known lepadomorphs and verucomorphs. Further subdivisions of lb types may be possible as more larvae are described. For example, *Lepas* and *Pollicipes* larvae (Table 2) have a broad flat-edge lb while chthamalids have a tapered tongue-shaped lb.

Five of the North Inlet species studied (Fig. 33) are part of the Balanus amphitrite complex. Within this complex of closely reared species or subspecies it is possible to derive two natural groupings and three subgroups (Henry and McLaughlin 1975). Based on statistical analysis of adult characteristics, B. amphitrite, B. eburneus, B. improvisus, and B. subalbidus were placed together in the "Amphitrite group." Henry and McLaughlin considered B. amphitrite and B. improvisus least similar within this group with B. subalbidus and B. eburneus intermediate between them. A similar pattern exists for the nauplii of these species. Balanus eburneus and B. improvisus larvae are difficult to distinguish while B. subalbidus and B. amphitrite nauplii are similar but relatively distinct from the first species pair. The fifth member of the complex found in North Inlet, B. venustus, was placed in a separate subgroup by Henry and McLaughlin. Larvae of this species, with proportionally long caudal spine, lateral spines, and dorsal spines, are quite distinct from other larvae of the complex, thus supporting the grouping of adults.

Balanus venustus nauplii more closely resemble those of Conopea galeata during early stages, but unlike C. galeata, lateral and dorsal carapace spines become progressively smaller at each molt and by stage VI are essentially lost. The particularly large dorsal spine of C. galeata larvae is unique for presently described balanid larvae; however, the long AP and DTS, large fh, and well-developed abdominal spines are evident in other larae of the subfamily Archaeobalaninae (Acasta, hirona, Eliminius, Solidobalanus—Table 2).

The coronulid Chelonibia was long considered a rimative balanid but has recently been reclassified Newman and Ross 1976). Although most adults of this coup are extremely specialized obligatory commensals Ross and Newman 1967), C. patula will settle on both rustaceans and shells; its larvae may be typical of the enus but perhaps, like the adult, are a less specialized orm. The first and second stage nauplii of C. testuinaria, the only other larvae of the genus described, are uite similar to C. patula larvae (Pillai 1958). The sigificance of the distinctly pigmented gut region of C. atula larvae is unknown. If this represents yolk cells, C. atula may be evolving a lecithotrophic mode of developent. The bulky body with highly arched carapace is milar to the form of lecithotrophic Scalpellum scalellum larvae.

Features other than the large globular body closely reemble those of Balanoidea larvae. Setation and setal ypes are typical; AP spination is similar, but additional pines rarely seen in *Balanus* are present. This feature lso occurs in the coronuloid *Tetraclita karandei* Karande 1974b). Of particular note is the retention of PSS An1 terminal setal pattern in all naupliar stages. Intennular setation tends to be extremely conservative a cirriped nauplii and this variation makes *C. patula* arvae unique for balanomorphs.

Chthamalid larvae differ in many aspects from coronubid and balanoid larvae and perhaps more closely reemble lepadomorph larvae. All chthamalid larvae have ispid and feathery setae and a unilobed lb. At least 16 etae are present on the An2 endopod of stage VI nauplii f all chthamalid and most lepadomorph larvae, but no more than 14 setae occur in balanid larvae (Table 17). Chthamalus fragilis nauplii, like other described larvae

Table 17.—Setal counts for the antennae of stage VI nauplii of some barnacle species. "F" indicates feathered setae are present.

	Number of setae					
Species	exopod	endopod				
Coronulaidea						
Chelonibia patula	12	14				
Tetraclita purascens	10	14				
Balanoidea						
Eliminius modestus	12	14				
Conopea galeata	11	14				
Balanus balanus	9	11				
Balanus eburneus	12	14				
Chthamaloidea						
Chthamalus fragilis	12	18F				
C. stellatus	12	18F				
Ç. aestuarii	12	19F				
Octomeris angulosa	12	17F				
Chamaesipho columna	12	17F				
C. brunnea	12	16F				
Other						
Verruca stroemia	12	16F				
Pollicipes polymerus	12	16F				
Lepas fascicularis	12	16F				
Nauplius Y	12	19F				
Octolasmis muelleri	11	10				

in the genus (Table 2), lack PS spines and have lost the DTS by stage VI. The nauplii of the pedunculate barnacle, *Ibla cumingi*, bear a striking resemblance to *C. fragilis* and *C. stallatus* (Bassindale 1936) larvae, but the sketchy description (Karande 1974c) of *Ibla* nauplii prevents a detailed comparison.

Octolasmis muelleri and O. forrestii larvae appear atypical in many aspects. In general appearance the nauplii most closely resemble Lepas larvae and indeed, the poecilasmatid Octolasmis is considered to be closely related to the Lepadae (Newman et al. 1969). As indicated in the figures of Lepas fascicularis nauplii (Bainbridge and Roskell 1966), Lepas, like Octolasmis, has bristled setae on the An1 (a feature presently unique to these two groups). Octolasmis larvae, however, lack AP spination, have a unique tapered lb, exhibit reduced setal numbers on the An2 (Table 17), and have a much reduced Mn. The cs does not develop a posterior border until stage V. None of these features are shared with larvae of other barnacle species. The significance or possible advantage of these modifications in Octolasmis larvae is unknown. The reduction of the Mn and presence of specialized setal types on the An1 infers a possible modification of the general feeding behavior described for balanid larvae (see Rainbow and Walker 1976). The swimming pattern in Octolasmis nauplii consists of a slow sweeping movement of the appendages as opposed to a much more rapid beat for balanoid nauplii. It appears likely that there are fundamental differences in swimming and feeding behavior.

Nauplius SC clearly demonstrates the present limited knowledge of cirriped larvae. Although the most common cirriped larval type in offshore plankton samples examined, nauplius SC does not closely resemble any larvae of known origin (Table 2). The unilobed lb, feathered setae, and An2 setation clearly excludes it from coronuloid and balanoid species. The tapered lb, small size in later stages, and furcal structure run counter to known features of *Lepas* larvae. The lack of teeth on the lb and absence of hispid setae also make it a doubtful chthamaloid species. Although the size and lb resemble *Octolasmis* larvae, the short fh and appendages do not.

Nauplius SC thus appears to originate from one of the numerous lepadomorph or verrucomorph families with unknown larval types. If its larvae are equally predominant at other times of the year, positive identification would be of interest both for larval biology and cirriped species distribution.

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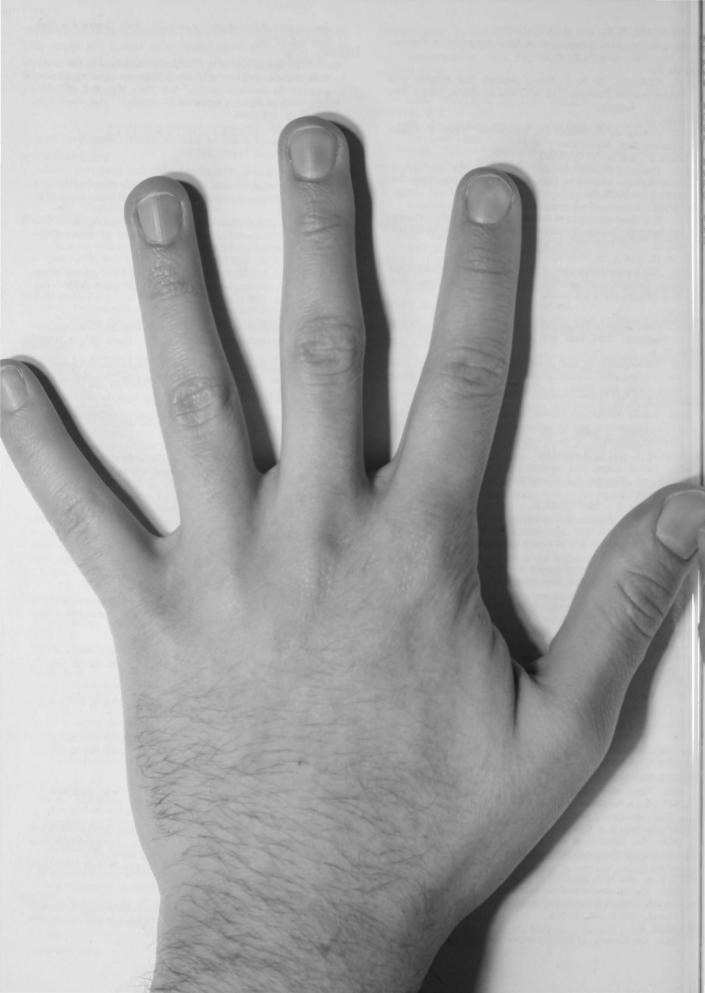
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